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The phylogeny of pholcid spiders: a critical evaluation of relationships suggested by molecular data (Araneae, Pholcidae)

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Abstract

With almost 600 species, the latest molecular phylogeny of pholcid spiders (Eberle et al. 2018, BMC Evolutionary Biology) more than triples the largest previously available molecular phylogeny of the family. At the level of genera, the coverage is high (86%, i.e., 75 of the 87 named genera), and at the level of subfamilies it is complete. The present paper is an effort to critically evaluate the implications of this phylogeny for pholcid systematics. The analyses largely support the division of Pholcidae into five subfamilies: Ninetinae, Arteminae, Modisiminae, Smeringopinae, and Pholcinae. Their compositions are largely unchanged except that *Chisosa* Huber, 2000 is moved from Ninetinae to Arteminae. The positions of *Artema* Walckenaer, 1837 and *Priscula* Simon, 1893 in this system remain dubious. Relationships among subfamilies remain weakly supported, except for the sister group relationship between Smeringopinae and Pholcinae. Several major clades within subfamilies are separated from each other along geographical boundaries; for example within Modisiminae a South American clade and a Central + North American + Caribbean clade, and within Smeringopinae a Sub-Saharan clade and a clade ranging from the Mediterranean to Central Asia. Central + North American + Caribbean clades in both Ninetinae and Modisiminae may originate from South American ancestors.

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Many taxonomic changes are suggested by the data, some of which are formally implemented herein. Two new genera result from the splitting of *Calapnita* Simon, 1892 and *Panjange* Deeleman-Reinhold & Deeleman, 1983, respectively: *Nipisa* Huber, **gen. n.**; and *Apokayana* Huber, **gen. n.** Nine new genera result from splitting of *Pholcus*: *Cantikus* Huber, **gen. n.**; *Kelabita* Huber, **gen. n.**; *Kintaqa* Huber, **gen. n.**; *Muruta* Huber, **gen. n.**; *Meraha* Huber, **gen. n.**; *Paiwana* Huber, **gen. n.**; *Pribumia* Huber, **gen. n.**; *Teranga* Huber, **gen. n.**; and *Tissahamia* Huber, **gen. n.** Two genera are newly synonymized: *Platnicknia* Özdikmen & Demir, 2009 is synonymized with *Modisimus* Simon, 1893; *Sihala* Huber, 2011 is synonymized with *Pholcus* Walckenaer, 1805. *Pholcus agadir* Huber, 2011 is moved to *Micropholcus* Deeleman-Reinhold & Prinsen, 1987, resulting in the new combination *Micropholcus agadir* (Huber, 2011).

Keywords
Biogeography, phylogeny, systematics, taxonomy

Introduction

Pholcidae is among the most species-rich spider families (World Spider Catalog 2018) and includes some of the spiders best known to the general public due to their occurrence in houses all over the world. Large amounts of morphological, taxonomic, behavioural, and biogeographic data on pholcids have been gathered and published over the last decades (http://www.pholcidae.de). Pholcidae is emerging as an ecologically highly diverse family that includes representatives with exceptional morphology and behaviour (e.g., asymmetric genitalia, ocular area modifications; highly regular webs; wrapping of prey with sticky silk; Huber and Nuñeza 2015, Huber et al. 2016c, Deeleman-Reinhold 1986a, Huber 2005b, Japyassú and Macagnan 2004), and that in some parts of the world is either extremely abundant (e.g., in East African forests; Sørensen et al. 2002) or has extreme levels of endemism (e.g., in Brazil's Atlantic Forest; Huber and Rheims 2011, Huber 2015, 2016, 2018). However, convincing evolutionary interpretations are often impeded by insufficient phylogenetic resolution and by large gaps in the taxon sampling. The most recent molecular phylogeny of Pholcidae (Eberle et al. 2018) is undoubtedly a major step forward. Under the assumption that a good sample of taxa is possibly more important than an increase of characters/genes (cf. Graybeal 1998, Heath et al. 2008) we more than tripled the number of species as compared to the previous phylogeny of Dimitrov et al. (2013); many genera and major species groups were included for the first time. As far as the percentage of named genera included is concerned (86%), this is probably the most comprehensive molecular phylogeny of any major spider family so far. Despite this substantial increase in taxon sampling which has greatly improved our understanding of pholcid relationships, our tree remains a mosaic of 'good' and 'bad' parts: some nodes receive high support, others receive low or essentially no support. Revealingly, some support values changed dramatically among preliminary analyses of the present data. For example, unexpected clades with maximum support but contradicting any other evidence (e.g., morphology) suggested the existence of paralog

sequences. In other cases, doubts persist but we were not able to identify problems with the molecular data. The idea of the present paper is thus to complement the primary phylogenetic data in Eberle et al. (2018) with a detailed account of arachnological implications and to look not only at but also beyond support values; we compare the molecular phylogeny with phylogenies derived from cladistic analysis of morphological characters and other information, and distinguish between clades that we consider a solid basis for further work and clades that we consider in need of further phylogenetic research.

Material and methods

The trees presented here are derived from mitochondrial and nuclear gene sequences (12S, 16S, 18S, 28S, CO1, H3) gathered from 597 species of Pholcidae plus 32 outgroup species representing nine entelegyne and ten non-entelegyne families. For detailed specimen data, primers, lab protocols, alignment and tree inference algorithms, see Eberle et al. (2018). The present evaluation is based on four trees resulting from maximum likelihood analyses of data sets with varying degrees of missing data and unstable taxa, using two algorithms (RAxML, Stamatakis 2014; IQ-TREE, Nguyen et al. 2015). For the complete set of taxa, RAxML found the tree with the highest likelihood while the tree inferred with IQ-TREE was in better concordance with the known morphological evidence as suggested by cladistic analyses of morphological data and by qualitative character assessment (detailed in the respective sections below). Further trees were inferred with RAxML based on a reduced data set without rogue taxa (RogueNaRok, Wilkinson 1996, Sanderson and Shaffer 2002, Aberer et al. 2013) and on a "4+ genes" data set, including only those taxa for which four or more of the six target genes were available.

We calculated three types of branch support values for all trees: standard bootstrapping (SBS), rapid bootstrapping (RBS; Stamatakis et al. 2008), and Shimodaira–Hasegawa-like approximate likelihood ratio test (SH-like aLRT; Guindon et al. 2010). Terminal taxa are composed of a consistent string of five variables: (1) unique specimen code; (2) genus name, either scientific name, unique code, or "Gen. n." for putatively new genera; (3) species name, either scientific name or unique code; (4) code for vial containing the specimen; (5) x's and o's, to respectively clarify the presence or absence of loci in the following order: 12S, 16S, 18S, 28S, CO1, H3.

We chose the tree from the IQ-TREE analysis for illustration and annotation because it appears more congruent with morphology. For the sake of clarity, only the RBS support is shown here; it may reflect true support most accurately (Anisimova et al. 2011). The same tree with all support values but without additional annotations is available as Supplementary file, together with the trees derived from RAxML from the complete and the two reduced, i.e., RogueNaRok, and "4+ genes" data sets.

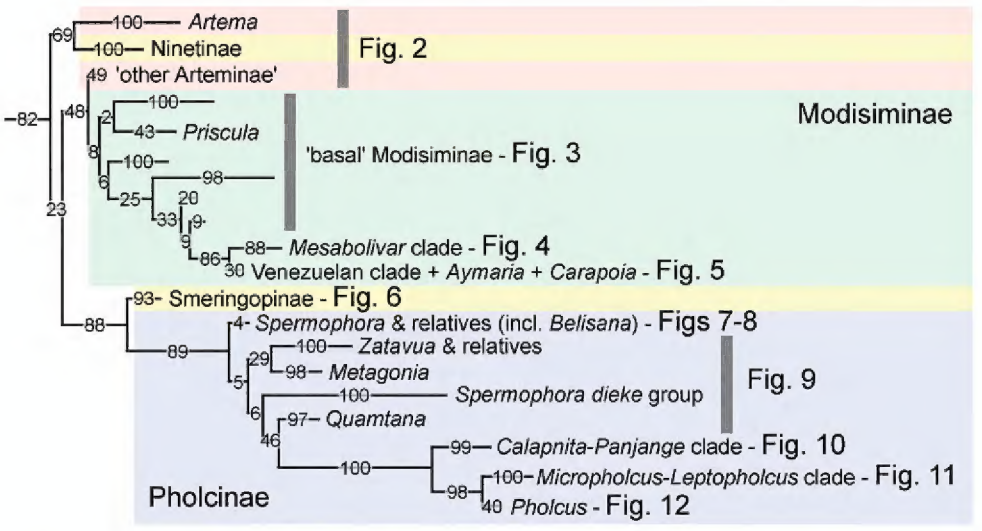


Figure 1. Backbone of the pholcid tree shown in Figs 2–12, derived from IQ-TREE analysis of the complete dataset.

To avoid overloading the text with numbers, we generally refer to the RBS support as follows: "low" (<70), "modest" (70–79), "reasonable" (80–94), "high" (95–99), or "full" (100) support. Even though the resolution of pholcid phylogeny has improved dramatically since 2011, the formal classification (Huber 2011b) into five subfamilies is not changed (Figure 1). Between the taxonomic levels of subfamilies and species we prefer to use informal names rather than tribes, subtribes, etc. Such unranked and formally unnamed taxa are less likely to burden future work as long as several major groups are still weakly supported and likely to change in composition or to be entirely rejected. The word "clade" is used like monophylum; thus, a clade can consist of subclades and those subclades are clades that again can consist of subclades. In general, colours in the phylogenies have no meaning beyond supporting the visual recognition of clades. The only exception is with *Belisana* Thorell, 1898, where litter and leaf-dwelling representatives are marked with different colours. Genus and species counts include the formal taxonomic changes herein. All measurements are in mm.

Systematic accounts

Subfamily Ninetinae Simon, 1890

Figure 2

Ninetinae Simon, 1890: 95. Type genus *Ninetis* Simon, 1890, by monotypy. Huber 2011b: 212.

Remarks. Ninetinae are small to tiny ground-dwelling spiders that are largely restricted to arid environments (Huber and Brescovit 2003; BA Huber, unpublished data). With only 31 described extant species, the subfamily is by far the smallest of the five currently recognized subfamilies in Pholcidae. Ninetinae seem to be diverse in the New World (ten named genera + about four unnamed genera; BA Huber,

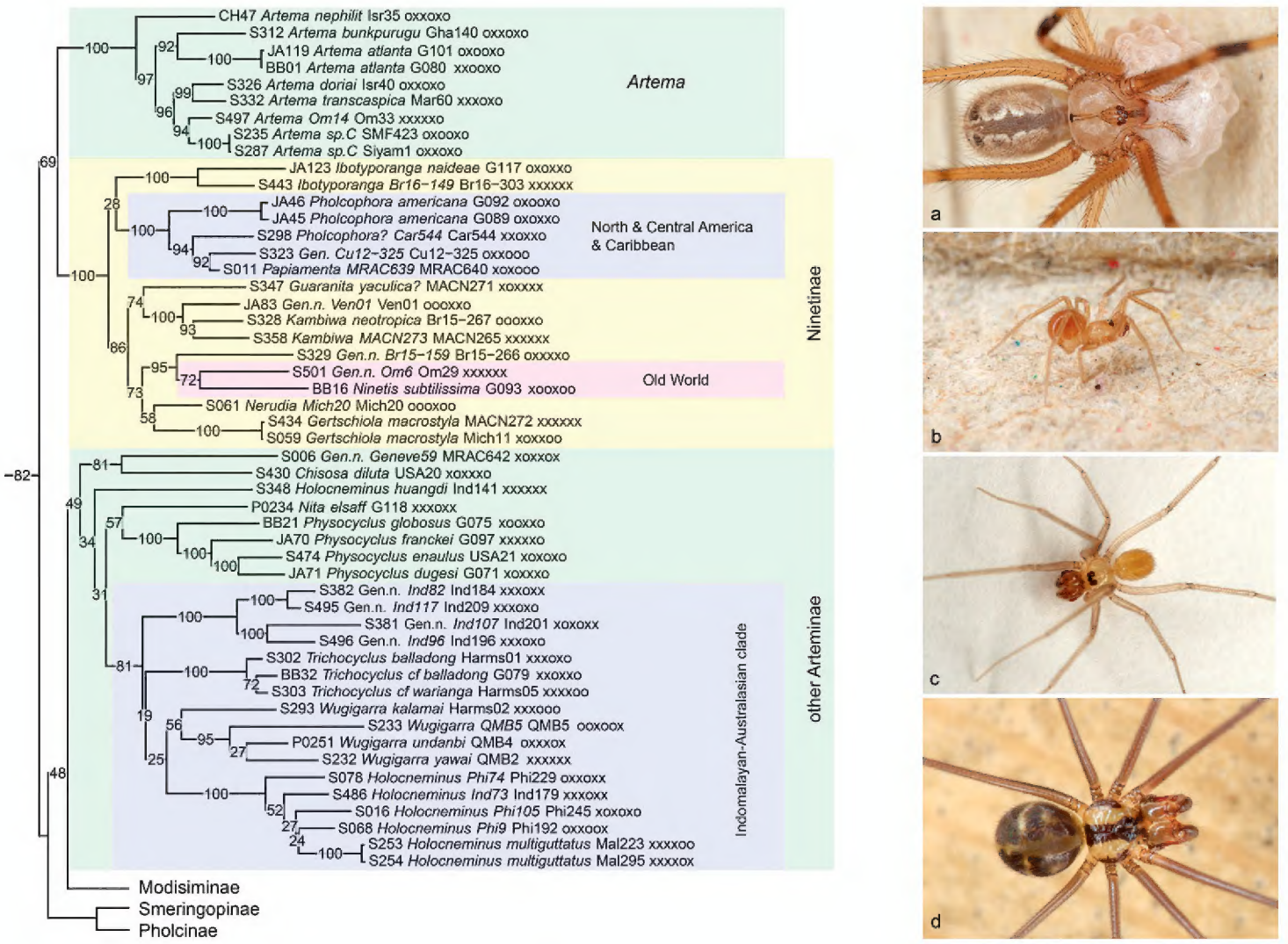

CH47 Artema nephilit Isr35 oxxoxo
S312 Artema bunkpurugu Gha140 oxxoxo
JA119 Artema atlanta G101 oxooxo
BB01 Artema atlanta G080 xxooxo
S326 Artema doriai Isr40 oxxoxo
S332 Artema transcaspica Mar60 xxxoxo
S497 Artema Om14 Om33 xxxxxo
S235 Artema sp.C SMF423 oxooxo
S287 Artema sp.C Siyam1 oxxoxo
Artema
JA123 Ibotyporanga naideae G117 oxoxxo
S443 Ibotyporanga Br16−149 Br16−303 xxxxxx
JA46 Pholcophora americana G092 oxooxo
JA45 Pholcophora americana G089 oxoxxo
S298 Pholcophora? Car544 Car544 xxoxxo
S323 Gen. Cu12−325 Cu12−325 oxxooo
S011 Papiamenta MRAC639 MRAC640 xoxooo
North & Central America & Caribbean
S347 Guaranita yaculica? MACN271 xoxxxx
JA83 Gen.n. Ven01 Ven01 oooxxo
S328 Kambiwa neotropica Br15−267 oooxxo
S358 Kambiwa MACN273 MACN265 xxxxxx
S329 Gen.n. Br15−159 Br15−266 oxxxxo
S501 Gen.n. Om6 Om29 xxxxxx
BB16 Ninetis subtilissima G093 xooxoo
Old World
S061 Nerudia Mich20 Mich20 oooxoo
S434 Gertschiola macrostyla MACN272 xxxxxx
S059 Gertschiola macrostyla Mich11 xoxxoo
Ninetinae
S006 Gen.n. Geneve59 MRAC642 xoxxox
S430 Chisosa diluta USA20 xoxxxo
S348 Holocneminus huangdi Ind141 xxxxxx
P0234 Nita elsaff G118 xxxoxx
BB21 Physocyclus globosus G075 xooxxo
JA70 Physocyclus franckei G097 xxxxxo
S474 Physocyclus enaulus USA21 xoxoxo
JA71 Physocyclus dugesi G071 xoxxxo
S382 Gen.n. Ind82 Ind184 xxxoxx
S495 Gen.n. Ind117 Ind209 xxxoxo
S381 Gen.n. Ind107 Ind201 xoxoxx
S496 Gen.n. Ind96 Ind196 xxxoxo
S302 Trichocyclus balladong Harms01 xxxoxo
BB32 Trichocyclus cf balladong G079 xxoxxo
S303 Trichocyclus cf warianga Harms05 xxxxoo
S293 Wugigarra kalamai Harms02 xxxooo
S233 Wugigarra QMB5 QMB5 ooxoox
P0251 Wugigarra undanbi QMB4 oxxxox
S232 Wugigarra yawai QMB2 xxxxxx
S078 Holocneminus Phi74 Phi229 oxxoxx
S486 Holocneminus Ind73 Ind179 xxxoxx
S016 Holocneminus Phi105 Phi245 xoxoxo
S068 Holocneminus Phi9 Phi192 oxxoox
S253 Holocneminus multiguttatus Mal223 xxxxoo
S254 Holocneminus multiguttatus Mal295 xxxxox
Indomalayan-Australasian clade
other Arteminae
Modisiminae
Smeringopinae
Pholcinae
a
b
c
d

Figure 2. Ninetinae and Arteminae **a** *Artema* sp. n. "Om14" (Oman) **b** Gen. n. (Ninetinae) sp. n. "Om6" (Oman) **c** *Chisosa diluta* (USA) **d** Gen. n. (Arteminae) sp. n. "Ind82" (Sulawesi).

unpublished data) where they represent the most southern (Argentina) and most northern (Canada) autochthonous pholcid records worldwide. Only two genera (*Ninetis* Simon, 1890 and one unnamed; BA Huber, unpublished data) are known from the Old World.

Their short legs make them superficially strikingly different from 'typical' long-legged pholcids. This distinctness was recognized as early as 1893, when Eugène Simon classified the only ninetine species available to him in a separate subfamily "Ninetidinae", as opposed to all other pholcids classified in Pholcinae (Simon 1893). Subsequent morphological and molecular phylogenies have partly supported this view (Huber 2000, Dimitrov et al. 2013) but never convincingly with strong support.

Our present analyses include 15 species representing eight of the eleven described genera, originating from both the New World and the Old World (Figure 2). A sister-group relationship between Ninetinae and all other pholcids is not supported by our analyses. Instead, all four analyses put Ninetinae as sister to *Artema* Walckenaer, 1837, and this clade is in turn sister to all other pholcids. For reasons discussed below (under Arteminae), we consider this relationship between *Artema* and Ninetinae dubious. The conclusion here is that Ninetinae are 'basal', either with *Artema* or without, but in any case the external relationships of Ninetinae remain unsatisfactorily resolved and need further study.

The monophyly of the subfamily receives high to full support in all analyses but the composition is slightly different from previous concepts: the North American *Chisosa* Huber, 2000, originally thought to be a representative of Ninetinae (Huber 2000), is moved to Arteminae. This move is also supported by male genitalic characters (massive palpal femur; procursus with dorsal apophysis and ventral pocket) and by somatic characters (exposed tarsal organ; reduction of epiandrous spigots; Huber 2000). Another genus that was previously (Huber and El Hennawy 2007, Huber 2011b) thought to be a member of Ninetinae is *Nita* Huber & El Hennawy, 2007. As already suggested in a previous analysis (Dimitrov et al. 2013), *Nita* is not a member of Ninetinae but of Arteminae.

The internal relationships of Ninetinae suggested by the molecular data are difficult to evaluate: they are mostly neither supported nor contradicted by morphological data. Two details are remarkable because they suggest that South America may not only be the most diverse region as far as Ninetinae are concerned but also the ancestral region of the subfamily. First, the analyses fully support a monophyletic North and Central American/Caribbean clade (*Pholcophora* Banks, 1896; *Papiamenta* Huber, 2000; and unidentified taxa from Cuba and Puerto Rico; "clade 2e" in Huber 2011b) that is either nested among South American ancestors or is sister to the South American *Ibotyporanga* Mello-Leitão, 1944 (with reasonable support in the 4+ genes tree only). Based on its geographic distribution, we predict that the Mexican *Tolteca* is also a member of this clade. Second, the two Old World genera (*Ninetis* and an undescribed genus from Oman) are also sister taxa (with low to modest support) and in all analyses (except for the 4+ genes analysis where *Ninetis* is missing) nested among South American taxa.

Subfamily Arteminae Simon, 1893
Figure 2

Artemeae Simon, 1893: 463. Type genus *Artema* Walckenaer, 1837, by monotypy.
Arteminae Simon; Huber 2011b: 212.

Remarks. All our analyses exclude the name-giving genus *Artema* from the clade containing all other Arteminae and invariably place *Artema* as sister to Ninetinae (Figure 2), formally precluding the use of the name Arteminae for this clade. We do not propose a new subfamily name for this clade but treat it as 'other Arteminae' because we consider the position of *Artema* dubious. *Artema* shares with 'other Arteminae' a unique pair of structures on the procursus: a ventral pocket and a dorsal apophysis. These structures are associated with asymmetric palp insertion in both species studied with respect to this detail [*Physocyclus globosus* (Taczanowski, 1874), *Artema nephilit* Aharon et al., 2017: Huber and Eberhard 1997, Aharon et al. 2017]. The structures are present in all Arteminae, even in taxa that were previously thought to be representatives

of other subfamilies, such as *Chisosa* and *Nita* (previously in Ninetinae; see above), and *Wugigarra* Huber, 2001 (previously in Modisiminae; see below) (Huber 2000, 2001, Huber and El Hennawy 2007). By contrast, these structures are apparently absent in all other Pholcidae. Curiously and unexplainable to us, previous molecular analyses have supported a position of *Artema* among 'other Arteminae' (Astrin et al. 2007: fig. 1, Dimitrov et al. 2013).

Some of the 99 currently known species of Arteminae are relatively large spiders with long, strong legs and high globose abdomens. The genus *Artema*, in particular, includes probably the largest pholcids in terms of body mass (Aharon et al. 2017). However, tiny species that were previously assigned to Ninetinae partly because of their size (*Chisosa*, *Nita*) are now included in Arteminae, and their 'basal' position in the cladogram suggests that ancestral Arteminae may in fact have been tiny. Just like Ninetinae, Arteminae often occur in rather dry regions, sometimes even in deserts like the Australian *Trichocyclus* Simon, 1908. They have a wide distribution, but are apparently absent from Sub-Saharan Africa and from South America (except for "Geneve59", a tiny undescribed species representing a new undescribed genus on Curaçao and Aruba).

The monophyly of 'other Arteminae' is supported in all our analysis, even though with low support (possibly because of the dubious position of *Artema*, see above). Similar to our previous analysis (i.e. except for the position of *Artema*; Dimitrov et al. 2013), 'other Arteminae' is sister to Modisiminae, with variable support (reasonable support only in the RogueNaRok tree; in other trees, bootstrap support is low but SH values range from 82 to 99). This sister group relationship is weakly supported by morphology: 'other Arteminae' and Modisiminae lack epiandrous spigots. However, epiandrous spigots have been lost several times convergently in Pholcidae (Huber 2000, BA Huber, unpubl. data).

Internal relationships in 'other Arteminae' are partly resolved with reasonable support. The data suggest a large Indomalayan-Australasian clade, including the genera *Trichocyclus* and *Wugigarra* (Australia), *Holocneminus* Berland, 1942 (SE Asia and Pacific; excluding the misplaced and highly isolated *H. huangdi* Tong & Li, 2009), and a new undescribed genus (without any described species; ranging from Eastern Indonesia to the Pacific). Sister to this clade is either the New World genus *Physocyclus* Simon, 1893 alone or *Physocyclus* together with the Middle-Eastern monotypic *Nita*. However, support values for any of these options are low and morphological data do not favour (nor contradict) any of them. Finally, the 'basal' branches, i.e., those leading to the taxa outside the Indomalayan-Australasian clade and *Physocyclus* (and *Nita* in the case of the IQ-TREE analysis) lead to a group of North American and Caribbean taxa (the North American genus *Chisosa* being sister to a tiny undescribed species representing a new undescribed genus on Curaçao and Aruba: "Geneve59"), and to the SE-Asian *Holocneminus huangdi*, an isolated species that appears misplaced also by morphological criteria (A Valdez-Mondragón, pers. comm., Nov. 2015).

Subfamily Modisiminae Simon, 1893
Figs 3–5

Modisimeae Simon, 1893: 484. Type genus *Modisimus* Simon, 1893, by subsequent designation (Huber 2011b).
Modisiminae Simon; Huber 2011b: 216.

Remarks. Modisiminae are the typical pholcids of the humid Neotropics, where they occupy a wide variety of microhabitats from leaf litter to high among the vegetation. This ecological variability is paralleled by a wide range of body forms, from tiny ground-dwelling forms (e.g., Gertsch 1982, Huber and Rheims 2011) to some of the largest pholcids with leg spans of over 15 cm (e.g., Huber and Astrin 2009, Huber 2015, 2018). With currently 480 species in 24 genera, Modisiminae is one of the two large subfamilies of Pholcidae, with several species-rich genera (e.g., *Anopsicus* Chamberlin & Ivie, 1938; *Psilochorus* Simon, 1893; *Modisimus* Simon, 1893; *Mesabolivar* González-Sponga, 1998; *Carapoia* González-Sponga, 1998) and many undescribed species.

All previous analyses have supported this group (Huber 2000, 2001, Bruvo Mađarić et al. 2005, Dimitrov et al. 2013), even though with minor differences in composition. The equivalent 'New World clade' in Huber (2001) still included the Australian *Wugigarra*, a genus that has since been moved to Arteminae (Dimitrov et al. 2013). As a result, Modisiminae is now considered to be restricted to the New World.

Our analyses all recover Modisiminae, but with very low support values. This is possibly due to the mysterious Andean genus *Priscula* Simon, 1893 (Figure 3) that is either included in Modisiminae (IQ-TREE) or not (RAxML). The position of *Priscula* has always been considered problematic. Simon (1893) created a separate taxon "Prisculeae" for this genus; Brignoli (1981) synonymized it with *Physocyclus*; the first morphological cladistic analysis (Huber 2000) supported the position of *Priscula* near *Physocyclus* but this result was explicitly doubted (Huber 2000: 129). In the molecular analysis of Dimitrov et al. (2013) *Priscula* was excluded because the positions of the included species varied dramatically among different types of analyses. Morphologically, *Priscula* differs from (other) Modisiminae by the presence of ALS piriform gland spigots and by the absence of a retrolateral apophysis on the male palpal coxa (Huber 2000), i.e., it has retained plesiomorphic characters. A sister-group relationship between *Priscula* and other Modisiminae appears thus plausible from a morphological point of view.

Despite the low support values, we thus consider Modisiminae (including *Priscula* or not) a likely monophyletic group. Several morphological characters support Modisiminae (incl. *Priscula*): an exposed tarsal organ; the reduction of epiandrous spigots (shared with 'other Arteminae'; see above); and a large distance between ALE and PME (Huber 2000). As indicated above (section Arteminae) our data weakly support a sister-group relationship between 'other Arteminae' and Modisiminae.

Within Modisiminae, many support values are extremely low, and the suggested relationships are thus unreliable (Figure 3). In addition, taxon sampling is very uneven,

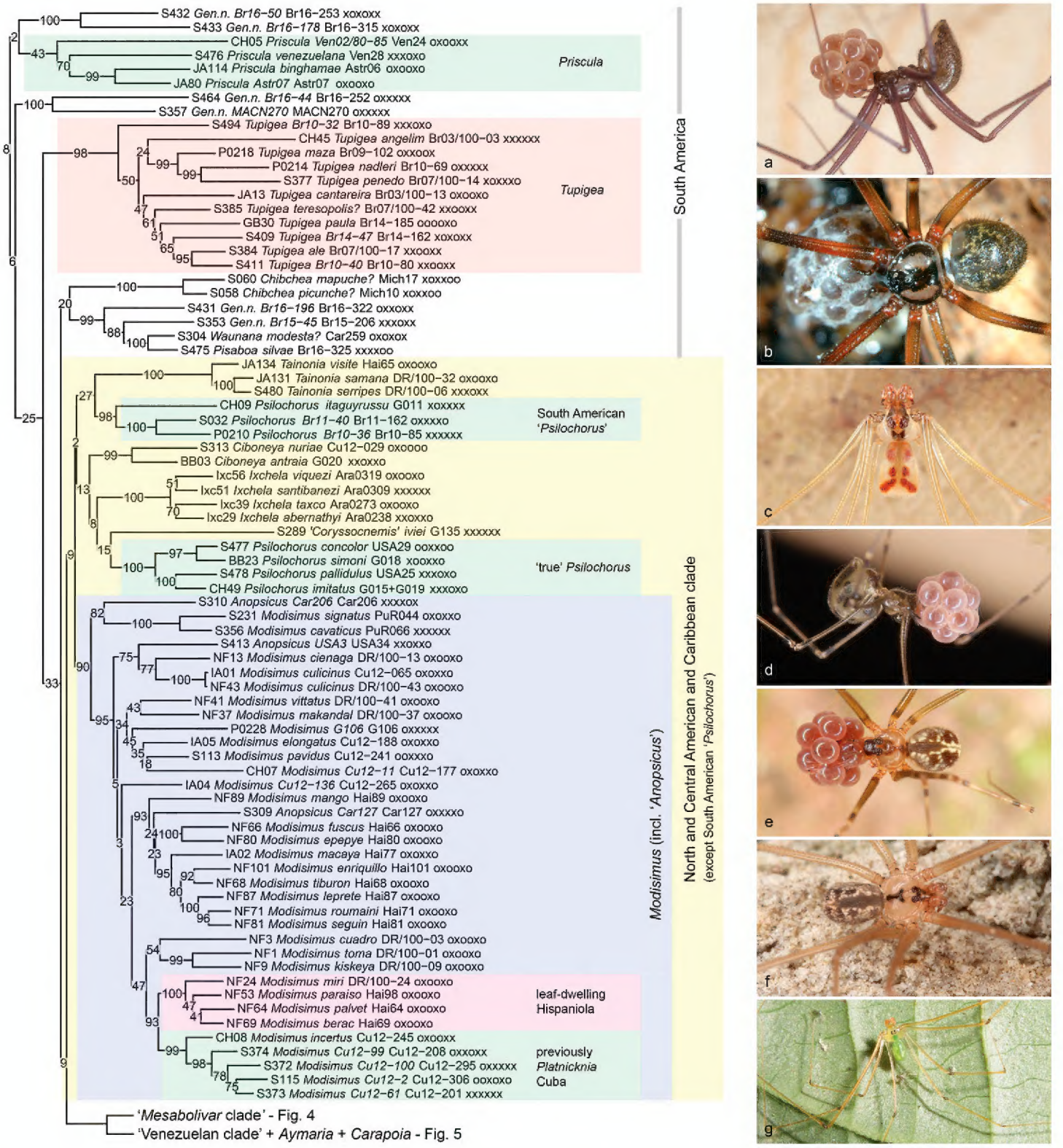

S432 Gen.n. Br16–50 Br16–253 xoxoxx
S433 Gen.n. Br16–178 Br16–315 xoxoxx
CH05 Priscula Ven02/80–85 Ven24 oxooxx
S476 Priscula venezuelana Ven28 xxxoxo
JA114 Priscula binghamae Astr06 oxooxo
JA80 Priscula Astr07 Astr07 oxooxo
Priscula
S464 Gen.n. Br16–44 Br16–252 oxxxxx
S357 Gen.n. MACN270 MACN270 oxxxxx
S494 Tupigea Br10–32 Br10–89 xxxoxo
CH45 Tupigea angelim Br03/100–03 xxxxxx
P0218 Tupigea maza Br09–102 oxxoox
P0214 Tupigea nadleri Br10–69 oxxxxx
S377 Tupigea penedo Br07/100–14 xoxxxo
JA13 Tupigea cantareira Br03/100–13 oxooxo
S385 Tupigea teresopolis? Br07/100–42 xxooxx
GB30 Tupigea paula Br14–185 ooooxo
S409 Tupigea Br14–47 Br14–162 xoxoxx
S384 Tupigea ale Br07/100–17 xxooxx
S411 Tupigea Br10–40 Br10–80 xxooxx
Tupigea
S060 Chibchea mapuche? Mich17 xoxxoo
S058 Chibchea picunche? Mich10 xoxxoo
S431 Gen.n. Br16–196 Br16–322 oxxoxx
S353 Gen.n. Br15–45 Br15–206 xxxoxx
S304 Waunana modesta? Car259 oxoxox
S475 Pisaboa silvae Br16–325 xxxxoo
South America
JA134 Tainonia visite Hai65 oxooxo
JA131 Tainonia samana DR/100–32 oxooxo
S480 Tainonia serripes DR/100–06 xxxoxx
CH09 Psilochorus itaguyrussu G011 xoxxxx
S032 Psilochorus Br11–40 Br11–162 oxxxxo
P0210 Psilochorus Br10–36 Br10–85 xxxxxx
South American 'Psilochorus'
S313 Ciboneya nuriae Cu12–029 oxoooo
BB03 Ciboneya antraia G020 xxoxxo
Ixc56 Ixchela viquezi Ara0319 oxooxo
Ixc51 Ixchela santibanezi Ara0309 xxxxxx
Ixc39 Ixchela taxco Ara0273 oxooxo
Ixc29 Ixchela abernathyi Ara0238 xxoxxo
S289 'Coryssocnemis' iviei G135 xxxxxx
S477 Psilochorus concolor USA29 ooxxoo
BB23 Psilochorus simoni G018 xooxxo
S478 Psilochorus pallidulus USA25 xxxxxo
CH49 Psilochorus imitatus G015+G019 xxxxxo
'true' Psilochorus
S310 Anopsicus Car206 Car206 xxxxxx
S231 Modisimus signatus PuR044 oxoxxo
S356 Modisimus cavaticus PuR066 xxxxxx
S413 Anopsicus USA3 USA34 xxoxxo
NF13 Modisimus cienaga DR/100–13 oxooxo
IA01 Modisimus culicinus Cu12–065 oxoxxo
NF43 Modisimus culicinus DR/100–43 oxooxo
NF41 Modisimus vittatus DR/100–41 oxooxo
NF37 Modisimus makandal DR/100–37 oxooxo
P0228 Modisimus G106 G106 oxxxxx
IA05 Modisimus elongatus Cu12–188 oxoxxo
S113 Modisimus pavidus Cu12–241 ooxxxo
CH07 Modisimus Cu12–11 Cu12–177 oxoxxo
IA04 Modisimus Cu12–136 Cu12–265 oxoxxo
NF89 Modisimus mango Hai89 oxooxo
S309 Anopsicus Car127 Car127 oxxxxo
NF66 Modisimus fuscus Hai66 oxooxo
NF80 Modisimus epepye Hai80 oxooxo
IA02 Modisimus macaya Hai77 oxoxxo
NF101 Modisimus enriquillo Hai101 oxooxo
NF68 Modisimus tiburon Hai68 oxooxo
NF87 Modisimus leprete Hai87 oxooxo
NF71 Modisimus roumaini Hai71 oxooxo
NF81 Modisimus seguin Hai81 oxooxo
NF3 Modisimus cuadro DR/100–03 oxooxo
NF1 Modisimus toma DR/100–01 oxooxo
NF9 Modisimus kiskeya DR/100–09 oxooxo
NF24 Modisimus miri DR/100–24 oxooxo
NF53 Modisimus paraiso Hai98 oxooxo
NF64 Modisimus palvet Hai64 oxooxo
NF69 Modisimus berac Hai69 oxooxo
leaf-dwelling Hispaniola
CH08 Modisimus incertus Cu12–245 oxooxx
S374 Modisimus Cu12–99 Cu12–208 oxxoxx
S372 Modisimus Cu12–100 Cu12–295 oxxxxx
S115 Modisimus Cu12–2 Cu12–306 ooxoxo
S373 Modisimus Cu12–61 Cu12–201 xxxxxx
previously Platnicknia Cuba
Modisimus (incl. 'Anopsicus')
North and Central American and Caribbean clade (except South American 'Psilochorus')
'Mesabolivar clade' - Fig. 4
'Venezuelan clade' + Aymaria + Carapoia - Fig. 5
a
b
c
d
e
f
g

Figure 3. 'Basal' Modisiminae **a** Gen. n., sp. n. "Br16-50" (Brazil) **b** *Priscula andinensis*? (Venezuela) **c** Gen. n., sp. n. "Br16-196" (Brazil) **d** *Tupigea* sp. n. "Br14-47" (Brazil) **e** *Pisaboa silvae* (Brazil) **f** *Psilochorus imitatus* (USA) **g** *Modisimus incertus* (Cuba).

with some genera well represented (e.g., *Carapoia*, *Mesabolivar*, *Modisimus*), and others poorly represented or entirely missing (see below). However, several results are consistent among analyses and noteworthy for various reasons: they suggest groups that appear feasible in terms of biogeography; they suggest interesting evolutionary scenarios; and they suggest formal taxonomic changes, some of which have been suggested before based on morphology.

Apart from *Priscula*, the 'basal' branches within Modisiminae lead to small South American unnamed taxa (Figure 3). In particular, the two species "Br16-44" and

"MACN270" are both tiny, with body lengths of 0.9 and 1.3 mm, respectively. Other 'basal' branches lead to an unnamed Amazonian genus ("Br16-178" and "Br16-50"; body lengths: 1.5–1.8 mm) and the Atlantic Forest genus *Tupigea* Huber, 2000 (body lengths: 1.3–1.9 mm; Huber 2000, Huber and Rheims 2011). This suggests a similar evolutionary scenario as proposed for 'other Arteminae' above, i.e., that ancestral Modisiminae may have been small ground-dwelling species. *Priscula* is once again the disturbing factor in this scenario: all known representatives of *Priscula* are medium-size to large spiders (Huber 2000), possibly surpassed (as far as body mass is concerned) by *Artema* only. In both Arteminae and Modisiminae, the emerging picture is one of medium-sized forms missing or disappearing early, large forms experiencing little subsequent changes in body shape and poor subsequent speciation (*Artema*: currently eight species; *Priscula*: currently 17 species), and small forms diversifying dramatically in size, shape, and numbers ('other Arteminae': currently 91 species; Modisiminae without *Priscula*: currently 463 species).

The next branch (Figure 3; *Chibchea* Huber, 2000 to *Pisaboa* Huber, 2000) includes several South American genera, some of them diverse but poorly represented in our analyses (e.g., *Chibchea*). The close relationship between *Pisaboa* and *Waunana* Huber, 2000 was already suggested in the original descriptions of these genera (Huber 2000), even though based on highly homoplastic characters (vertical hairs on male leg tibiae in high density; shape of apophysis on male palpal femur). A close relationship of these two genera with *Chibchea* either receives very low support (IQ-TREE, RAxML) or is not recovered (RogueNaRok); it is neither supported nor contradicted by morphology. Clearly, this clade needs a much denser sampling and the addition of missing taxa that are possibly related (e.g., *Pomboa*).

The next clade (Figure 3) includes all North and Central American and Caribbean taxa, suggesting that the ancestor of this clade arrived in the region from South America. This scenario was explicitly rejected by Dimitrov et al. (2013) based on the supposed age of the group (~120–170 Ma). However, our upcoming analysis has not been able to confirm this age (Eberle et al. 2018; we were not able to calculate convincing absolute ages from the data). The clade is recovered in most analyses (it is paraphyletic in the 4+ genes tree) but always with low support (only SH values are reasonable to high). The only geographic outlier in this clade is South American '*Psilochorus*'. North American ('true') *Psilochorus* and South American '*Psilochorus*' each receive high to full support but are never resolved as sister taxa. Whether South American '*Psilochorus*' are ancestral within this large clade or represent a case of back-colonization is currently impossible to say; the internal nodes in this clade have partly too low support to favour a particular scenario. The inclusion of the Central American *Ixchela* Huber, 2000 in this clade fits the geographic pattern and contradicts a previous speculation (in Huber 2000) that *Ixchela* might be close to the South American genus *Aymaria* Huber, 2000. In much the same way, the only Central American representative of *Coryssocnemis* Simon, 1893 included in our analyses is placed in this group, far away from 'true' South American *Coryssocnemis* (the polyphyly of *Coryssocnemis* has long been suspected: Gertsch 1971, Brignoli 1981, Huber 1998, 2000). The Cuban endemic

genus *Platnicknia* Özdikmen & Demir, 2009 is deeply nested within the large genus *Modisimus*. It is resolved as sister to a distinctive group of Hispaniolan leaf-dwelling representatives of *Modisimus* (the "leaf-dwelling species group" in Huber et al. 2010) and synonymized below. Finally, the large genus *Anopsicus* (63 described species) is poorly represented in our analyses. The three species included are all undescribed, do not group together, and are nested among *Modisimus*. Since neither the type species of *Anopsicus* is included nor is a potential close relative (or at least another species from Yucatán), the monophyly and position of *Anopsicus* both remain dubious.

Sister to the previous North and Central American and Caribbean clade is another large, entirely South American clade (Figure 3, bottom). The sister-group relationship is very poorly supported, but the monophyly of the South American clade has modest (4+ genes) to reasonable (RogueNaRok) support. It is divided into three subclades with reasonable to full support plus the genus *Aymaria* that is represented by a single species and whose position within this clade is not convincingly resolved. The first subclade included is here informally called the '*Mesabolivar* clade' (Figure 4); the second subclade is largely Venezuelan and thus called 'Venezuelan clade' (Figure 5); the third subclade is the genus *Carapoia* (Figure 5).

Within the '*Mesabolivar* clade' (Figure 4), our analyses suggest two specific relationships that are likely to have drastic taxonomic consequences. First, *Litoporus* Simon, 1893 is nested among 'true' northern South American *Mesabolivar*. This has been suggested before (Dimitrov et al. 2013), but that previous analysis included a single species of *Litoporus* whose generic identity was uncertain (Huber et al. 2013). The present analyses include several unambiguous (Amazonian) representatives of *Litoporus*. Our data support the monophyly of *Litoporus* (full support) but also its position within *Mesabolivar* (reasonable to high support). Second, *Mesabolivar* is composed of two sub-clades: 'true' northern South American *Mesabolivar*, and southern South American (largely Atlantic Forest) '*Mesabolivar*'. The southern sub-clade includes the monotypic genus *Teuia* Huber, 2000 (synonymized with *Mesabolivar* in Huber 2018; the type species of *Teuia* is not included but a putatively closely related species: *M. sepitus*). Potential formal taxonomic changes are discussed in the Taxonomy section below. The close relationship between *Otavaloa* Huber, 2000 and *Mesabolivar* is neither supported nor contradicted by morphological data.

The 'Venezuelan clade' (Figure 5) receives high to full support and is composed of several genera that are either known from Venezuela only (*Systenita* Simon, 1893, *Stenosfemuraia* González-Sponga, 1998), from Venezuela and Trinidad and Tobago (*Coryssocnemis*), or from Venezuela plus neighboring countries (*Mecolaesthus* Simon, 1893). A close relationship among these genera had been suspected before based on morphology (Huber 2000), and molecular data have always supported this (Bruvo-Mađarić et al. 2005: 28S data and combined analysis; Dimitrov et al. 2013). Our data suggest that *Coryssocnemis* may be nested within *Mecolaesthus*, but our taxon sampling is weak, the topology is unstable (*Systenita* is either nested within *Mecolaesthus* or not), and several internal nodes in the clade have low support. Formally, *Coryssocnemis* still includes several obviously misplaced species: several Central American species (see

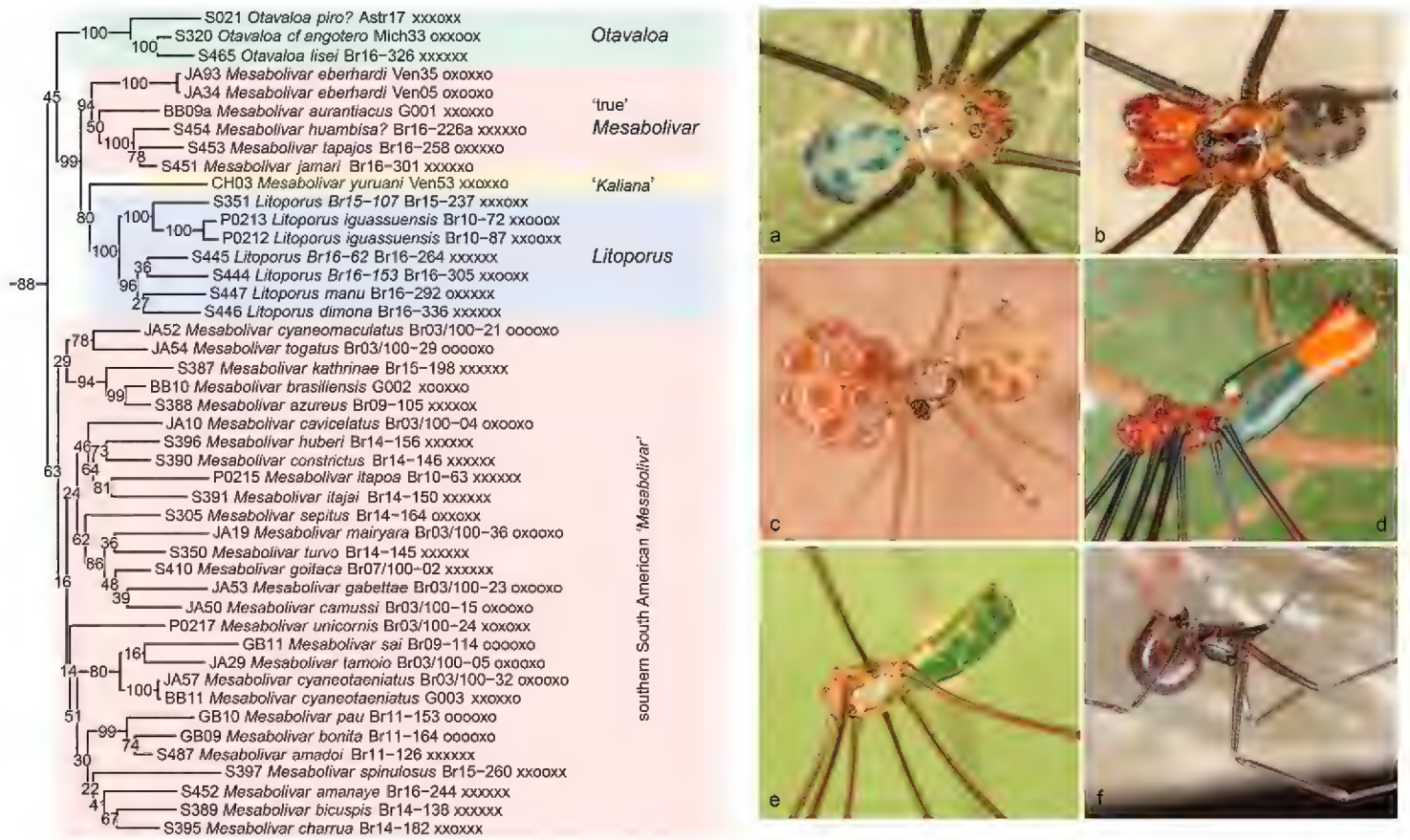

S021 Otavaloa piro? Astr17 xxxoxx
S320 Otavaloa cf angotero Mich33 oxxoox
S465 Otavaloa lisei Br16–326 xxxxxx
Otavaloa
JA93 Mesabolivar eberhardi Ven35 oxoxxo
JA34 Mesabolivar eberhardi Ven05 oxooxo
BB09a Mesabolivar aurantiacus G001 xxoxxo
S454 Mesabolivar huambisa? Br16–226a xxxxxo
S453 Mesabolivar tapajos Br16–258 oxxxxo
S451 Mesabolivar jamari Br16–301 xxxxxo
'true' Mesabolivar
CH03 Mesabolivar yuruani Ven53 xxoxxo
'Kaliana'
S351 Litoporus Br15–107 Br15–237 xxxoxx
P0213 Litoporus iguassuensis Br10–72 xxooox
P0212 Litoporus iguassuensis Br10–87 xxooxx
S445 Litoporus Br16–62 Br16–264 xxxxxx
S444 Litoporus Br16–153 Br16–305 xxooxx
S447 Litoporus manu Br16–292 oxxxxx
S446 Litoporus dimona Br16–336 xxxxxx
Litoporus
JA52 Mesabolivar cyaneomaculatus Br03/100–21 oooxxo
JA54 Mesabolivar togatus Br03/100–29 oooxxo
S387 Mesabolivar kathrinae Br15–198 xxxxxx
BB10 Mesabolivar brasiliensis G002 xooxxo
S388 Mesabolivar azureus Br09–105 xxxxox
JA10 Mesabolivar cavicelatus Br03/100–04 oxooxo
S396 Mesabolivar huberi Br14–156 xxxxxx
S390 Mesabolivar constrictus Br14–146 xxxxxx
P0215 Mesabolivar itapoa Br10–63 xxxxxx
S391 Mesabolivar itajai Br14–150 xxxxxx
S305 Mesabolivar sepitus Br14–164 oxxoxx
JA19 Mesabolivar mairyara Br03/100–36 oxooxo
S350 Mesabolivar turvo Br14–145 xxxxxx
S410 Mesabolivar goitaca Br07/100–02 xxxxxx
JA53 Mesabolivar gabettae Br03/100–23 oxooxo
JA50 Mesabolivar camussi Br03/100–15 oxooxo
P0217 Mesabolivar unicornis Br03/100–24 xoxoxx
GB11 Mesabolivar sai Br09–114 oooxxo
JA29 Mesabolivar tamoio Br03/100–05 oxooxo
JA57 Mesabolivar cyaneotaeniatus Br03/100–32 oxooxo
BB11 Mesabolivar cyaneotaeniatus G003 xxoxxo
GB10 Mesabolivar pau Br11–153 oooxxo
GB09 Mesabolivar bonita Br11–164 oooxxo
S487 Mesabolivar amadoi Br11–126 xxxxxx
S397 Mesabolivar spinulosus Br15–260 xxooxx
S452 Mesabolivar amanaye Br16–244 xxxxxx
S389 Mesabolivar bicuspis Br14–138 xxxxxx
S395 Mesabolivar charrua Br14–182 xxoxxx
southern South American 'Mesabolivar'
a
b
c
d
e
f

Figure 4. *Mesabolivar* clade **a** *Otavaloa lisei* (Brazil) **b** *Mesabolivar maraba* (Brazil) **c** *Litoporus* sp. n. "Br16-153" (Brazil) **d** *Mesabolivar cyaneotaeniatus* (Brazil) **e** *Mesabolivar kathrinae* (Brazil) **f** *Mesabolivar saci* (Brazil).

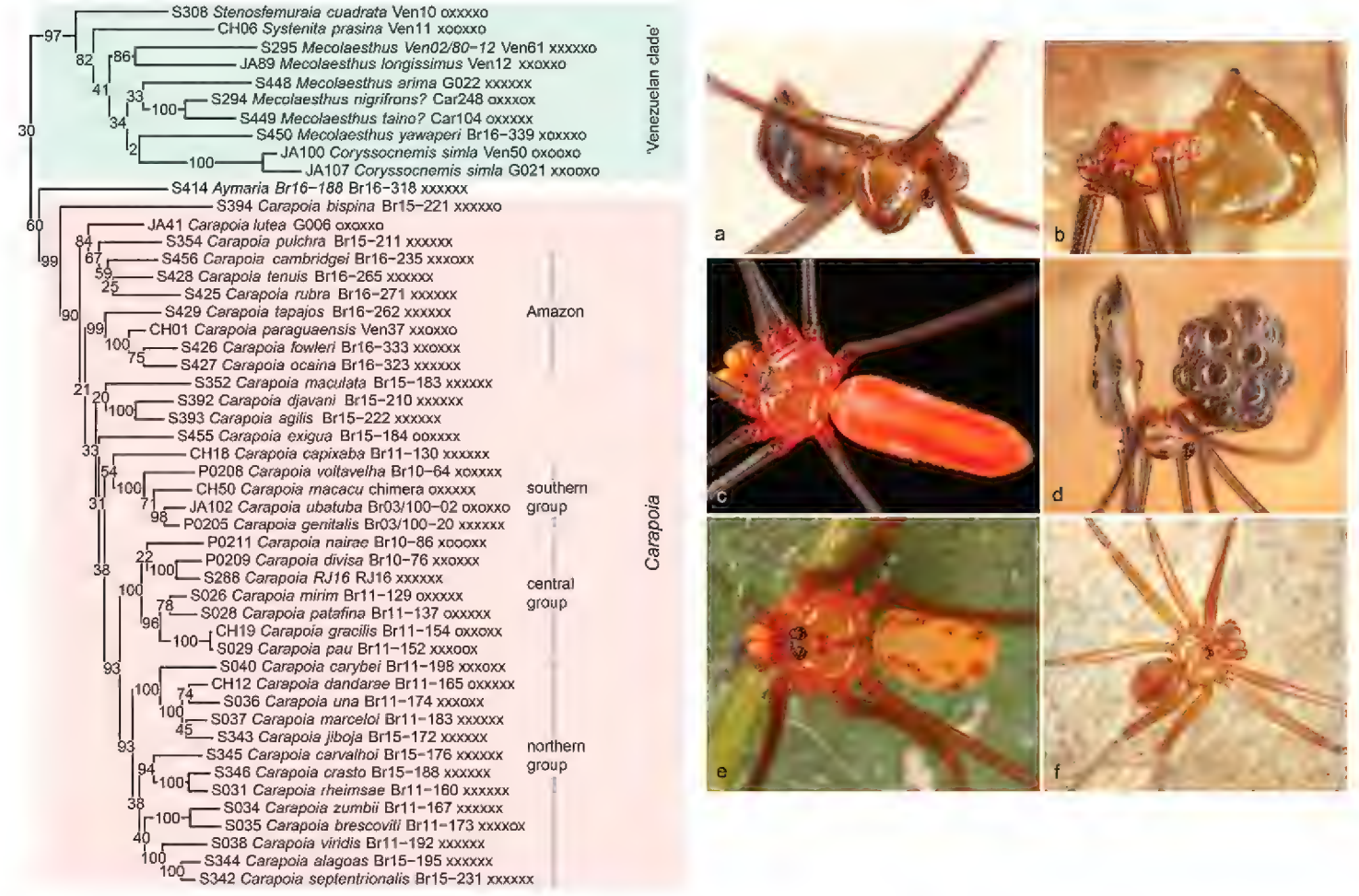

S308 Stenosfemuraia cuadrata Ven10 oxxxxo
CH06 Systenita prasina Ven11 xooxxo
S295 Mecolaesthus Ven02/80–12 Ven61 xxxxxo
JA89 Mecolaesthus longissimus Ven12 xxoxxo
S448 Mecolaesthus arima G022 xxxxxx
S294 Mecolaesthus nigrifrons? Car248 oxxxox
S449 Mecolaesthus taino? Car104 oxxxxx
S450 Mecolaesthus yawaperi Br16–339 xoxxxo
JA100 Coryssocnemis simla Ven50 oxooxo
JA107 Coryssocnemis simla G021 xxooxo
'Venezuelan clade'
S414 Aymaria Br16–188 Br16–318 xxxxxx
S394 Carapoia bispina Br15–221 xxxxxo
JA41 Carapoia lutea G006 oxoxxo
S354 Carapoia pulchra Br15–211 xxxxxx
S456 Carapoia cambridgei Br16–235 xxxoxx
S428 Carapoia tenuis Br16–265 xxxxxx
S425 Carapoia rubra Br16–271 xxxxxx
S429 Carapoia tapajos Br16–262 xxxxxx
CH01 Carapoia paraguaensis Ven37 xxoxxo
S426 Carapoia fowleri Br16–333 xxoxxx
S427 Carapoia ocaina Br16–323 xxxxxx
S352 Carapoia maculata Br15–183 xxxxxx
S392 Carapoia djavani Br15–210 xxxxxx
S393 Carapoia agilis Br15–222 xxxxxx
S455 Carapoia exigua Br15–184 ooxxxx
CH18 Carapoia capixaba Br11–130 xxxxxx
P0208 Carapoia voltavelha Br10–64 xxxxxx
CH50 Carapoia macacu chimera oxxxxx
JA102 Carapoia ubatuba Br03/100–02 oxoxxo
P0205 Carapoia genitalis Br03/100–20 xxxxxx
Amazon
southern group
P0211 Carapoia nairae Br10–86 xoooxx
P0209 Carapoia divisa Br10–76 xxoxxx
S288 Carapoia RJ16 RJ16 xxxxxx
S026 Carapoia mirim Br11–129 oxxxxx
S028 Carapoia patafina Br11–137 oxxxxx
CH19 Carapoia gracilis Br11–154 oxxoxx
S029 Carapoia pau Br11–152 xxxoox
central group
S040 Carapoia carybei Br11–198 xxxoxx
CH12 Carapoia dandarae Br11–165 oxxxxx
S036 Carapoia una Br11–174 xxxoxx
S037 Carapoia marceloi Br11–183 xxxxxx
S343 Carapoia jiboja Br15–172 xxxxxx
S345 Carapoia carvalhoi Br15–176 xxxxxx
S346 Carapoia crasto Br15–188 xxxxxx
S031 Carapoia rheimsae Br11–160 xxxxxx
S034 Carapoia zumbii Br11–167 xxxxxx
S035 Carapoia brescoviti Br11–173 xxxxox
S038 Carapoia viridis Br11–192 xxxxxx
S344 Carapoia alagoas Br15–195 xxxxxx
S342 Carapoia septentrionalis Br15–231 xxxxxx
northern group
Carapoia
a
b
c
d
e
f

Figure 5. Venezuelan clade + *Aymaria* + *Carapoia* **a** *Mecolaesthus yawaperi* (Brazil) **b** *Aymaria* sp. n. "Br16-188" (Brazil) **c** *Carapoia rubra* (Brazil) **d** *Carapoia kaxinawa* (Brazil) **e** *Carapoia pulchra* (Brazil) **f** *Carapoia agilis* (Brazil).

above), and several Atlantic Forest (Brazilian) species whose identity is probably impossible to resolve (poor descriptions, lost types; see Huber 2000, 2018).

The third subclade in the South American clade is *Carapoia* (Figure 5). Unlike *Mesabolivar* it is monophyletic and apparently less problematic, but just as *Mesabolivar*, the genus has become very difficult to diagnose, mainly because of 'untypical' species added to the genus based in large part on the present molecular data (Huber 2018). Both for *Mesabolivar* and *Carapoia* our analyses suggest several species groups that are also supported by morphological data. For a detailed discussion of these groups, see Huber (2018).

Subfamily Smeringopinae Simon, 1893
Figure 6

Smeringopodeae Simon, 1893: 474. Type genus *Smeringopus* Simon, 1890, by subsequent designation (Huber 2011b).
Smeringopinae Simon; Huber 2011b: 217.

Remarks. Smeringopinae is a relatively homogeneous subfamily (with respect to body shapes, colour, webs, and microhabitats), and in this sense similar to Ninetinae and Arteminae but very unlike Modisiminae and Pholcinae. Most of the 125 known species of Smeringopinae are medium-size to large, have long legs, elongated to cylindrical abdomens, and all have eight eyes. Another similarity to Ninetinae and Arteminae is that Smeringopinae are often found in rather arid regions. The most obvious exception is the largely humid tropical genus *Smeringopina* Kraus, 1957, which is also the genus with the smallest and largest representatives in the subfamily (with body lengths ranging from 2.5–10 mm) and with the widest range of microhabitats used (leaf litter to large sheltered spaces) (Huber 2013). The original distribution of the subfamily is Africa, the Mediterranean, and the Middle East. Three species have attained much wider distributions, resulting from human-mediated dispersal (Huber 2011b).

As in previous molecular analyses (Bruvo-Mađarić et al. 2005, Astrin et al. 2007, Dimitrov et al. 2013), Smeringopinae is sister to Pholcinae (Figure 1) with reasonable to high support. This relationship is also supported by morphology: the two taxa share tarsus IV comb-hairs spread over the entire length of the tarsus (Huber and Fleckenstein 2008).

The monophyly of Smeringopinae receives reasonable to high support in all our analyses. Previous molecular analyses have partly supported Smeringopinae, but also suggested rather obscure relationships [e.g., the position of *Holocnemus pluchei* (Scopoli, 1763) among Ninetinae in Astrin et al. 2007]. *Holocnemus pluchei* was included in preliminary analyses of the present data but its position was drastically unstable, so we decided to exclude it from the final analyses. Smeringopinae monophyly is rather weakly supported by morphology, i.e., by the presence of a large thoracic pit on the carapace (rather than a narrow furrow or an evenly domed carapace; cf. Huber 2011b).

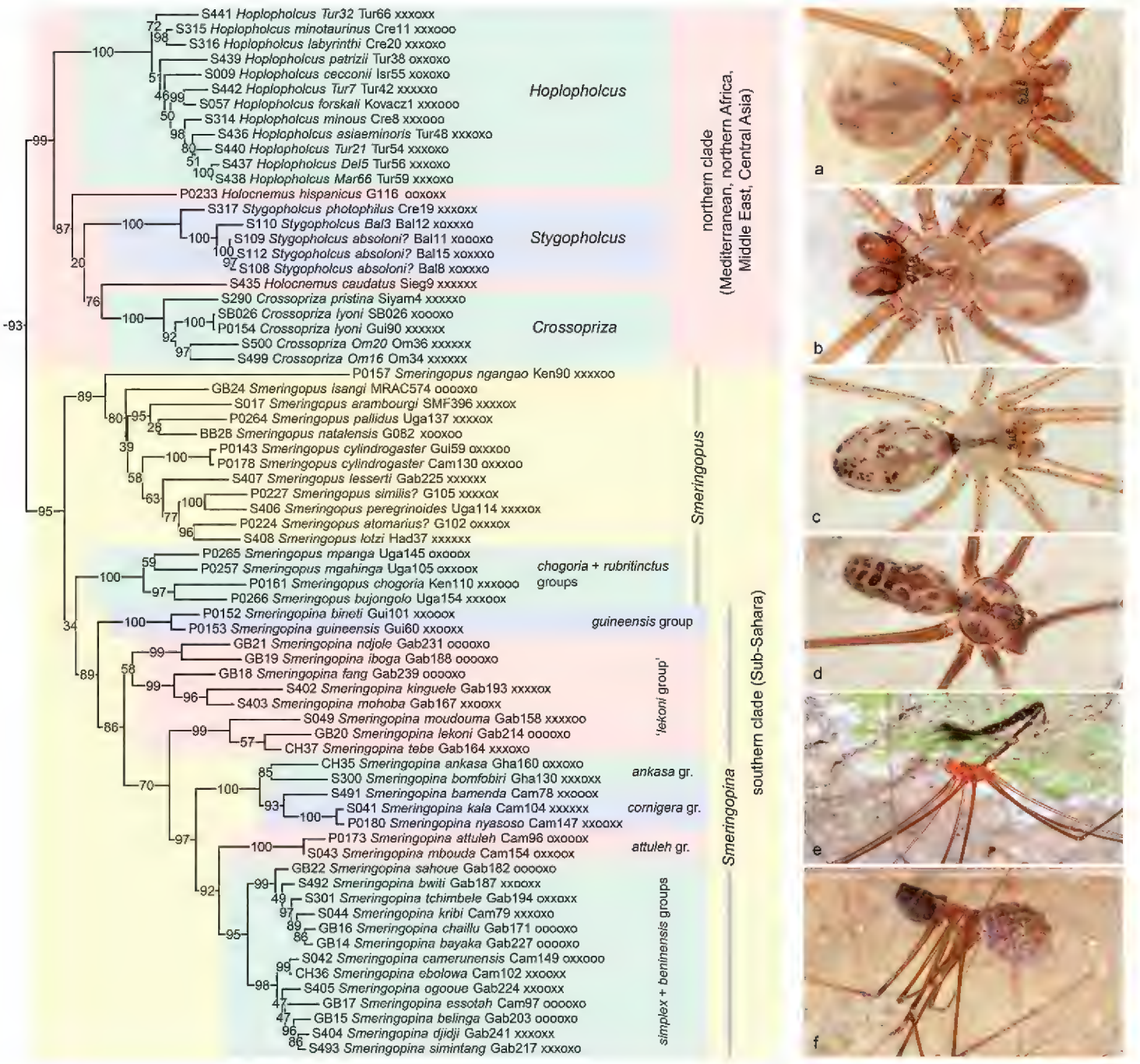

S441 Hoplopholcus Tur32 Tur66 xxxoxx
S315 Hoplopholcus minotaurinus Cre11 xxxooo
S316 Hoplopholcus labyrinthi Cre20 xxxoxo
S439 Hoplopholcus patrizii Tur38 oxxoxo
S009 Hoplopholcus cecconii Isr55 xoxoxo
S442 Hoplopholcus Tur7 Tur42 xxxxxo
S057 Hoplopholcus forskali Kovacz1 xxxooo
S314 Hoplopholcus minous Cre8 xxxooo
S436 Hoplopholcus asiaeminoris Tur48 xxxoxo
S440 Hoplopholcus Tur21 Tur54 xxxoxo
S437 Hoplopholcus Del5 Tur56 xxxoxo
S438 Hoplopholcus Mar66 Tur59 xxxoxo
Hoplopholcus
P0233 Holocnemus hispanicus G116 ooxoxx
S317 Stygopholcus photophilus Cre19 xxxoxx
S110 Stygopholcus Bal3 Bal12 xoxxxo
S109 Stygopholcus absoloni? Bal11 xooxxo
S112 Stygopholcus absoloni? Bal15 xoxxxo
S108 Stygopholcus absoloni? Bal8 xoxxxo
Stygopholcus
S435 Holocnemus caudatus Sieg9 xxxxxx
S290 Crossopriza pristina Siyam4 xxxxxo
SB026 Crossopriza lyoni SB026 xooxxo
P0154 Crossopriza lyoni Gui90 xxxxxx
S500 Crossopriza Om20 Om36 xxxxxx
S499 Crossopriza Om16 Om34 xxxxxx
Crossopriza
northern clade (Mediterranean, northern Africa, Middle East, Central Asia)
P0157 Smeringopus ngangao Ken90 xxxxoo
GB24 Smeringopus isangi MRAC574 oooxxo
S017 Smeringopus arambourgi SMF396 xxxxxx
P0264 Smeringopus pallidus Uga137 xxxxxx
BB28 Smeringopus natalensis G082 xooxoo
P0143 Smeringopus cylindrogaster Gui59 oxxxoo
P0178 Smeringopus cylindrogaster Cam130 oxxxoo
S407 Smeringopus lesserti Gab225 xxxxxx
P0227 Smeringopus similis? G105 xxxxox
S406 Smeringopus peregrinoides Uga114 xxxxox
P0224 Smeringopus atomarius? G102 oxxxxx
S408 Smeringopus lotzi Had37 xxxxxx
Smeringopus
P0265 Smeringopus mpanga Uga145 oxooox
P0257 Smeringopus mgahinga Uga105 oxxoox
P0161 Smeringopus chogoria Ken110 xxxooo
P0266 Smeringopus bujongolo Uga154 xxxoox
chogoria + rubritinctus groups
P0152 Smeringopina bineti Gui101 xxooox
P0153 Smeringopina guineensis Gui60 xxooxx
guineensis group
GB21 Smeringopina ndjole Gab231 oooxxo
GB19 Smeringopina iboga Gab188 oooxxo
GB18 Smeringopina fang Gab239 oooxxo
S402 Smeringopina kinguele Gab193 xxxxxx
S403 Smeringopina mohoba Gab167 xxooxx
'lekoni' group
S049 Smeringopina moudouma Gab158 xxxxoo
GB20 Smeringopina lekoni Gab214 oooxxo
CH37 Smeringopina tebe Gab164 xxxoxo
CH35 Smeringopina ankasa Gha160 oxxoxo
S300 Smeringopina bomfobiri Gha130 xxxxxx
ankasa gr.
S491 Smeringopina bamenda Cam78 xxooox
S041 Smeringopina kala Cam104 xxxxxx
P0180 Smeringopina nyasoso Cam147 xxooxx
cornigera gr.
P0173 Smeringopina attuleh Cam96 oxooox
S043 Smeringopina mbouda Cam154 oxxoox
attuleh gr.
GB22 Smeringopina sahoue Gab182 oooxxo
S492 Smeringopina bwiti Gab187 xxooxx
S301 Smeringopina tchimbele Gab194 oxxoxx
S044 Smeringopina kribi Cam79 xxxoxo
GB16 Smeringopina chaillu Gab171 oooxxo
GB14 Smeringopina bayaka Gab227 oooxxo
S042 Smeringopina camerunensis Cam149 oxxooo
CH36 Smeringopina ebolowa Cam102 xxooxx
S405 Smeringopina ogooue Gab224 xxooxx
GB17 Smeringopina essotah Cam97 oooxxo
GB15 Smeringopina belinga Gab203 oooxxo
S404 Smeringopina djidji Gab241 xxxoxx
S493 Smeringopina simintang Gab217 xxxoxo
simplex + beninensis groups
Smeringopina
southern clade (Sub-Sahara)
a
b
c
d
e
f

Figure 6. Smeringopinae **a** *Hoplopholcus* sp. n. "Mar66" (Turkey) **b** *Stygopholcus absoloni*? (Bosnia and Herzegovina) **c** *Crossopriza* sp. n. "Om11" (Oman) **d** *Smeringopus pallidus* (Philippines) **e** *Smeringopina pulchra* (Ghana) **f** *Smeringopina ankasa* (Ghana).

Within Smeringopinae, our data strongly support a basal split between a northern clade (Mediterranean, northern Africa, Middle East, Central Asia) and a southern clade (Sub-Sahara) (Figure 6). This basal split was also recovered in a morphological cladistic analysis (Huber 2012). Within the northern clade, *Hoplopholcus* Kulczynski, 1908 is sister to all other genera and not close to *Stygopholcus* Kratochvil, 1932 as repeatedly claimed by Brignoli (1971, 1976, 1979) but contested by Senglet (1971, 2001). The genera *Hoplopholcus*, *Stygopholcus*, and *Crossopriza* Simon, 1893 all receive full support, but the small Mediterranean genus *Holocnemus* Simon, 1873 (only three described species) continues to be problematic even after the exclusion of *H. pluchei*. The two species of *Holocnemus* included in our analyses never group together, and no morphological synapomorphy is known to suggest their sister-group relationship (in fact, *Holocnemus* has never been revised).

The southern (Sub-Saharan) clade includes *Smeringopus* Simon, 1890 and *Smeringopina*, and is also supported by a unique number of epiandrous spigots (two) (Huber 2012). The paraphyly of *Smeringopus* has been suggested before (Dimitrov et al. 2013), and our larger data set supports this view, but with low support values. Two of the species groups of *Smeringopus* proposed in Huber (2012) appear closer to *Smeringopina* than to other *Smeringopus*: the *chogoria* group and the *rubrotinctus* group. Morphological data do not support this view but they neither strongly contradict it: the two species groups lack the distinctive arrangement of pores on the pore plates (in groups or 'islands') and the retrolateral furrow on the male palpal femur present in all other species of *Smeringopus* (Huber 2012). Remarkably, *Smeringopus* and *Smeringopina* are largely separated geographically, with *Smeringopus* being most diverse in southern and eastern Africa, and *Smeringopina* in western and central Africa (Huber 2012, 2013). The *chogoria* and *rubrotinctus* groups are geographically restricted to an area where Central Africa (the Guineo-Congolian center of endemism) meets East Africa (Huber 2012). Other than that, our sampling in *Smeringopus* is not dense enough to test the species groups proposed in Huber (2012). Remarkably, though, the isolated 'basal' position of *S. ngangao* Huber, 2012 is supported by the present analyses.

Our analyses include 30 of the 44 described species of *Smeringopina* (68%), and all species groups proposed in Huber (2013) except two monotypic 'groups' (*S. fon* Huber, 2013; *S. ngungu* Huber, 2013). Even though for some species only one gene (CO1) was sequenced, our analyses support several species groups and deeper relationships proposed previously (Huber 2013), based on cladistic analysis of morphological characters. Morphology placed the West African *guineensis* group as sister to all other *Smeringopina*; all our analyses support both the monophyly of the *guineensis* group and its sister-group relationship with all other congeners. The next two branches are composed of representatives of the *lekoni* group, which is thus here considered paraphyletic rather than monophyletic. The *ankasa* and *cornigera* groups are both supported, as is their sister group relationship to each other. The *attuleh* group is supported, but not as sister to the *ankasa* + *cornigera* groups but as sister to the following group. The last clade is composed of representatives of the *simplex* and *beninensis* groups, but the clear dichotomy in the molecular trees is not equivalent to these groups. Instead, the *simplex* group includes all 'basal' representatives originally assigned to the *beninensis* group; the *beninensis* group includes only those species that have a light transversal element ventrally on the abdomen (character 9 in Huber 2013, which is thus less homoplastic than previously thought).

Subfamily Pholcinae C.L. Koch, 1850
Figs 7–12

Pholcidae CL Koch, 1850: 31. Type genus *Pholcus* Walckenaer, 1805, by monotypy.
Pholcinae CL Koch; Simon 1893: 461; Huber 2011b: 218.

Remarks. Pholcinae resemble Modisiminae in several respects. Their highest diversity is in the humid tropics and subtropics, and a large variety of body forms reflect adaptations to different microhabitats. With currently 922 species in 26 genera, Pholcinae is also similar to Modisiminae in diversity. In contrast to Modisiminae, Pholcinae is largely restricted to the Old World, with the notable exception of the New World endemic genus *Metagonia* Simon, 1893 and a few possibly relict species in *Pholcus* and *Micropholcus* (Huber 2011a, Huber et al. 2014). While only a single species of Modisiminae has followed humans around the globe [*Modisimus culicinus* (Simon, 1893)] and one further species has spread widely in Europe and neighboring regions [*Psilochorus simoni* (Berland, 1911)], several synanthropic species in Pholcinae have attained worldwide distributions or extended their ranges to another continent [most notably *Pholcus phalangioides* (Fuesslin, 1775); *Spermophora senoculata* (Dugès, 1836); *Micropholcus fauroti* (Simon, 1887); *Pholcus manueli* Gertsch, 1937].

The sister-group relationship between Pholcinae and Smeringopinae is well established (see above). The same is true for the monophyly of Pholcinae. All our analyses support this subfamily (reasonable to high support), and morphological data have also supported this group (presence of male lateral proximal cheliceral apophyses, Huber 1995, 2000; tarsus IV comb hairs in a single row, Huber and Fleckenstein 2008).

Even though Pholcinae are well represented in our analyses (317 of 597 species, i.e., 53%) internal relationships in this subfamily continue to be problematic. Several 'basal' nodes are poorly supported (Figure 1); in part the topology is highly sensitive to different algorithms of analysis; and some details appear dubious from the perspective of morphology. However, many details are strongly supported by morphology, including some deep nodes (e.g., the *Pholcus* group of genera); and some nodes, even though weakly supported or in conflict with morphology, provide reasonable and testable predictions for further research (e.g., the polyphyly of *Spermophora* Hentz, 1841; the close relationship of certain Sri Lankan taxa with African rather than Southeast Asian taxa; the monophyly of African *Pholcus*).

The subfamily is here divided into three operational groups, more for the sake of convenience than as a reflection of the support values they receive. Actually, support is low for all of them, but much of this division is consistent among different analyses and may well reflect real major groups. 'Group 1' (Figs 7, 8) is entirely composed of small six-eyed taxa, and is roughly equivalent to what was originally subsumed under the name *Spermophora*. 'Group 2' (Figure 9 part) is also entirely composed of six-eyed taxa and is remarkable because it places the exclusively New World genus *Metagonia* close to African and Madagascan taxa. 'Group 3' (Figure 9 part, Figs 10–12) includes the fully supported *Pholcus* group of genera as proposed previously (Huber 2011a) and its sister genus *Quamtana* Huber, 2003, a sister-group relationship that has also been proposed before (Huber 2003c). In the tree shown here (and in the RogueNaRok tree), the '*Spermophora' dieke* group has an isolated position outside of the three operational groups. In the other trees, it is part of 'group 1'.

Pholcinae 'group 1'
Figs 7, 8

Remarks. This group includes some genera named long ago, like *Spermophora*, *Belisana*, and *Paramicromerys* Millot, 1946. Most other genera were described relatively recently and resulted either from splitting of *Spermophora* (e.g., *Spermophorides* Wunderlich, 1992; *Buitinga* Huber, 2003; *Savarna* Huber, 2005; *Khorata* Huber, 2005) or from the discovery and description of new species (*Aetana* Huber, 2005; *Wanniyala* Huber & Benjamin, 2005; *Hantu* Huber, 2016).

A Southeast Asian clade that is consistently resolved with high to full support but variably placed either inside 'group 1' (IQ-TREE, RogueNaRok) or outside of the three operational groups as an isolated fourth group (4+ genes, RAxML) is composed of *Aetana*, Southeast Asian '*Spermophora*', and an undescribed new genus from Indonesia ("Ind206"). Morphological data have suggested a close relationship of *Aetana* with *Savarna*, *Khorata*, and *Hantu* (Huber et al. 2015). The positions of those three genera in our molecular trees are all unstable and problematic (see below). Thus, we consider it premature to conclude that the morphological data were misleading, and suggest that the positions of *Savarna*, *Khorata*, and *Hantu* need further analysis. A similar problem occurs with Southeast Asian '*Spermophora*'. The monophyly of the five species included receives reasonable to high support, but this group does not seem to be close to the type species *S. senoculata*. However, the position of *S. senoculata* varies strongly among analyses, and the idea that Southeast Asian taxa are in fact congeneric with *S. senoculata* (Huber 2005a) should not yet be discarded based on the present molecular data.

In *Aetana*, our analyses include 16 of 18 (89%) described species plus two undescribed species. The monophyly of the genus is highly to fully supported even though morphological support appeared weak (Huber et al. 2015). All four species groups proposed after cladistic analysis of morphological characters (Huber et al. 2015) are supported, but with different relationships among each other. Most of these relationships among species groups receive low support, but the *kiukoki* group is resolved as sister of the *omayan* group (with modest support) and this is in conflict with the results from morphology (Huber et al. 2015). The two unnamed subgroups within the *kinabalu* group and within the *omayan* group, respectively, proposed in Huber et al. (2015) are all recovered (with modest to full support).

The next clade within 'group 1' (Figure 7) includes three taxa whose position varies strongly among different analyses (see above): the type species of *Spermophora*, *S. senoculata*, and the Southeast Asian genera *Khorata* and *Savarna*. *Spermophora senoculata* is alternatively resolved as sister to the African '*Spermophora*' *akwamu* group (RAxML) or to the African '*Spermophora*' *kyambura* Huber & Warui, 2012 (4+ genes, RogueNaRok). Its sister group is essentially unknown. As indicated above, a close relationship with Southeast Asian '*Spermophora*', even though never recovered by our analyses, should not be definitely discarded. *Khorata* and *Savarna* are sister taxa in some analyses (low support; IQ-TREE, RogueNaRok), but wide apart in

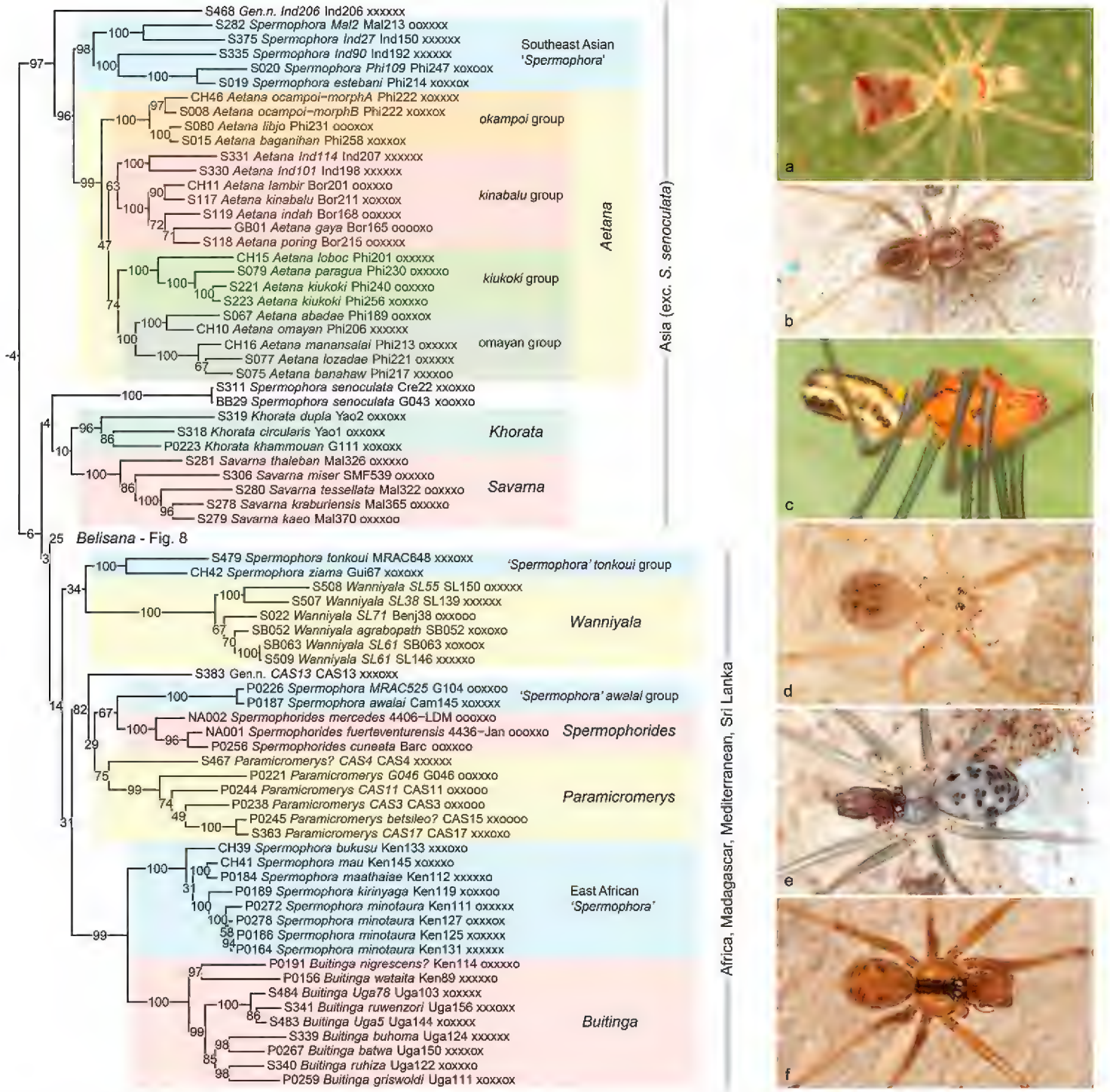

S468 Gen.n. Ind206 Ind206 xxxxxx
S282 Spermophora Mal2 Mal213 ooxxxx
S375 Spermophora Ind27 Ind150 xxxxxx
S335 Spermophora Ind90 Ind192 xxxxxx
S020 Spermophora Phi109 Phi247 xoxoox
S019 Spermophora estebani Phi214 xoxxox
Southeast Asian 'Spermophora'
CH46 Aetana ocampoi-morphA Phi222 xoxxxx
S008 Aetana ocampoi-morphB Phi222 xoxxox
S080 Aetana libjo Phi231 ooxoox
S015 Aetana baganihan Phi258 xoxxox
okampoi group
S331 Aetana Ind114 Ind207 xxxxxx
S330 Aetana Ind101 Ind198 xxxxxx
CH11 Aetana lambir Bor201 ooxxxo
S117 Aetana kinabalu Bor211 xoxxox
S119 Aetana indah Bor168 ooxxxx
GB01 Aetana gaya Bor165 ooooxo
S118 Aetana poring Bor215 ooxxxx
kinabalu group
CH15 Aetana loboc Phi201 oxxxxx
S079 Aetana paragua Phi230 oxxxxo
S221 Aetana kiukoki Phi240 ooxxxo
S223 Aetana kiukoki Phi256 xoxxxo
kiukoki group
S067 Aetana abedae Phi189 ooxxox
CH10 Aetana omayan Phi206 xxxxxx
CH16 Aetana manansalai Phi213 oxxxxx
S077 Aetana lozadae Phi221 oxxxxx
S075 Aetana banahaw Phi217 xxxxoo
omayan group
Aetana
S311 Spermophora senoculata Cre22 xxoxxo
BB29 Spermophora senoculata G043 xooxxo
S319 Khorata dupla Yao2 oxxoxx
S318 Khorata circularis Yao1 oxxoxx
P0223 Khorata khammouan G111 xoxoxx
Khorata
S281 Savarna thaleban Mal326 oxxxxo
S306 Savarna miser SMF539 oxxxxo
S280 Savarna tessellata Mal322 ooxxxo
S278 Savarna kraburiensis Mal365 oxxxxo
S279 Savarna kaeo Mal370 oxxxoo
Savarna
Asia (exc. S. senoculata)
Belisana - Fig. 8
S479 Spermophora tonkoui MRAC648 xxxoxx
CH42 Spermophora ziama Gui67 xoxoxx
'Spermophora' tonkoui group
S508 Wanniyala SL55 SL150 oxxxxx
S507 Wanniyala SL38 SL139 xxxxxx
S022 Wanniyala SL71 Benj38 oxxooo
SB052 Wanniyala agrabopath SB052 xoxoxo
SB063 Wanniyala SL61 SB063 xoxoox
S509 Wanniyala SL61 SL146 xxxxxo
Wanniyala
S383 Gen.n. CAS13 CAS13 xxxoxx
P0226 Spermophora MRAC525 G104 ooxxoo
P0187 Spermophora awalai Cam145 xoxxxx
'Spermophora' awalai group
NA002 Spermophorides mercedes 4406-LDM oooxxo
NA001 Spermophorides fuerteventurensis 4436-Jan oooxxo
P0256 Spermophorides cuneata Barc ooxxoo
Spermophorides
S467 Paramicromerys? CAS4 CAS4 xxxxxx
P0221 Paramicromerys G046 G046 ooxxxo
P0244 Paramicromerys CAS11 CAS11 oxxooo
P0238 Paramicromerys CAS3 CAS3 oxxooo
P0245 Paramicromerys betsileo? CAS15 xxooooo
S363 Paramicromerys CAS17 CAS17 xxxoxo
Paramicromerys
CH39 Spermophora bukusu Ken133 xxxoxo
CH41 Spermophora mau Ken145 xoxxxo
P0184 Spermophora maathaiae Ken112 xxxxxo
P0189 Spermophora kirinyaga Ken119 xoxxoo
P0272 Spermophora minotaura Ken111 oxxxxx
P0278 Spermophora minotaura Ken127 oxxxox
P0186 Spermophora minotaura Ken125 xoxxxx
P0164 Spermophora minotaura Ken131 xxxxxx
East African 'Spermophora'
P0191 Buitinga nigrescens? Ken114 oxxxxo
P0156 Buitinga wataita Ken89 xxxxxo
S484 Buitinga Uga78 Uga103 xoxxxx
S341 Buitinga ruwenzori Uga156 xxxoxx
S483 Buitinga Uga5 Uga144 xoxxxx
S339 Buitinga buhoma Uga124 xxxxxx
P0267 Buitinga batwa Uga150 xxxxox
S340 Buitinga ruhiza Uga122 xoxxxo
P0259 Buitinga griswoldi Uga111 xoxxox
Buitinga
Africa, Madagascar, Mediterranean, Sri Lanka
a
b
c
d
e
f

Figure 7. Pholcinae 'group 1' (*Spermophora* and relatives) **a** Gen. n., sp. n. "Ind206" (Halmahera); b, *Spermophora* sp. n. "Ind27" (Sumatra) **c** *Aetana baganihan* (Philippines) **d** *Spermophora senoculata* (Turkey) **e** *Savarna tessellata* (Thailand) **f** *Wanniyala agrabopath* (Sri Lanka).

others. The former result is considered more plausible for two reasons: (1) morphology supports a close relationship between *Khorata* and *Savarna* (Huber et al. 2015); (2) the alternative topology (4+ genes, RAxML) places the Southeast Asian *Savarna* as sister to an East African clade.

The large Asian genus *Belisana* (Figure 8) is well represented in our analyses (30 species) but seems to suffer from rogue taxa, paralogs, and/or other unidentified problems. Only the RogueNaRok tree resolves a monophyletic *Belisana*. In other analysis, either *Hantu* (RAxML) or *Hantu* and '*Spermophora*' *kyambura* are nested within *Belisana* (IQ-TREE). A close relationship between *Belisana* and *Hantu* (that is also suggested in the RogueNaRok tree) is strongly contradicted by morphology: several

characters support a close relationship between *Hantu*, *Khorata*, and *Savarna* (Huber et al. 2015). We have no explanation for the position of *Hantu* in our trees. Intriguingly, *H. niah* Huber, 2016 (but not *H. kapit* Huber, 2016) was placed in a clade together with *Khorata* and *Savarna* in preliminary analyses of the present data. On the other hand, the African '*Spermophora*' *kyambura* might indeed be close to *Belisana*. In fact, had it been collected in Southeast Asia, it would probably have been assigned to *Belisana*. It was tentatively assigned to *Spermophora* because African '*Spermophora*' were polyphyletic anyway and because the closest known record of *Belisana* was from India, more than 5000 km east. However, the position of '*Spermophora*' *kyambura* varies among analyses and should be considered unresolved.

Our sample of *Belisana* includes numerous representatives from different microhabitats (litter and leaves) and with different types of webs ('usual' pholcid domed sheets and highly regular 'curtain' webs; Figs 8e–f; see also Deeleman-Reinhold 1986a, Huber 2005b). The present data suggest multiple microhabitat shifts within *Belisana*, but note that many nodes within the genus have very low support values. These low values also impede a proper interpretation of the fact that the two species with a 'usual' domed web (marked with D in Figure 8) included in the analyses (*B.* "Mal77", *B. tambligan* Huber, 2005) are not 'basal' but nested among species with highly regular 'curtain' webs (marked with R in Figure 8) [confirmed for *B. bohorok* Huber, 2005; *B. leuser* Huber, 2005; *B.* "Bor85"; *B. junkoae* (Irie, 1997); *B. sabah* Huber, 2005; BA Huber, unpubl. data].

Except for the Sri Lankan genus *Wanniyala*, all remaining taxa of Pholcinae 'group 1' (Figure 7) are African, Madagascan, and Mediterranean. They are grouped together but with very low support. South African and Madagascan '*Spermophora*' were not available for sequencing and are thus not included in our analyses; we predict they are members of this clade. As mentioned above, some analyses (RAxML, 4+ genes) placed the East Asian genus *Savarna* within this clade; we consider this topology dubious.

A close relationship between the West African '*Spermophora*' *tonkoui* group and *Wanniyala* is suggested in all our analyses, even though with low support (only SH values are consistently at 96–97). This relationship is also supported by morphology: the two taxa share a hinged procursus with a membranous process arising from the proximal part (see Huber and Benjamin 2005: fig. 7, Huber 2003b: fig. 293, Huber and Kwapong 2013: fig. 101).

The following clade (Figure 7) places the Central African '*Spermophora*' *awalai* group as sister to the Macaronesian and Mediterranean genus *Spermophorides*, both together sister to the Madagascan genus *Paramicromerys*, and all together sister to an undescribed Madagascan genus ("CAS13"). Support for these relationships is modest, and the clade is different in composition in the 4+ genes tree (*Spermophorides* is missing from this analysis).

The last clade in Pholcinae 'group 1' is highly to fully supported in all analyses and includes the East African genus *Buitinga* and East African '*Spermophora*', each with full support in all analyses. The sister group relationship between these two taxa makes sense geographically but is not evident from morphology.

S417 Belisana ranong Mal361 xoxxxx
CH40 Spermophora kyambura Uga140 xxxoxx
P0174 Spermophora kyambura Cam101 xxxoox
S322 Hantu niah Bor226 ooxoxx
CH48 Hantu kapit Bor183 xoxxxx
Hantu
S498 Belisana SL37 SL123 oxxoxo
S103 Belisana Tai4 Tai67 xoxoxo
S334 Belisana Ind15 Ind140 xxxoxx
S239 Belisana ketambe? Mal303 xoxxoo
CH43 Belisana aninaj Mal352 xoxxxo
S230 Belisana australis Phi280 xoxxxx
S025 Belisana Benj44 Benj44 xxxoox
S249 Belisana Mal91 Mal290 xxxoxo
S333 Belisana bohorok Ind127 xxxoxx R
S242 Belisana leuser Mal304 xoxxxx R
P0282 Belisana Raff32 Raff32 oxxoox
P0231 Belisana akebona G109 xxxoox
S248 Belisana Mal77 Mal279 xxxxxx D
S129 Belisana Bor85 Bor185 xxooox R
S244 Belisana Mal30 Mal241 xoxoxo
S237 Belisana junkoae Tai62 xoxxoo R
S128 Belisana Bor160 Bor169 oxxoox
S127 Belisana Bor152 Bor166 oxxxxx
S247 Belisana Mal76 Mal278 xxoxxo
S126 Belisana Bor147 Bor216 ooxxoo
S416 Belisana Mal35 Mal243 xxxxoo
S246 Belisana Mal55 Mal252 oxxxoo
S337 Belisana sandakan Ind139 xoxxoo
S336 Belisana nahtanoj Ind181 xxxxxx
S241 Belisana khaoyai Mal344 xoxxox
S338 Belisana tambligan Ind213 xxxxxx D
S219 Belisana Phi80 Phi234 xooxox
S386 Belisana sabah Bor214 xxxxxx R
S125 Belisana Bor121 Bor198 ooxxxx
S243 Belisana Bor121 Mal203 xxxxox
a
b
c
d
e
f

Figure 8. *Belisana* and *Hantu*. For *Belisana*, the background colours signify microhabitat: red = ground; green = leaf. D, domed web; R, highly regular 'curtain' web. Photos **a** *Hantu niah* (Sarawak) **b** *Hantu kapit* (Sarawak) **c** *Belisana sandakan* (Sumatra) **d** *Belisana sabah* (Sabah) **e** domed web of *Belisana* sp. n. "Mal77" (Malaysia) **f** regular 'curtain' web of *Belisana bohorok* (Sarawak).

Pholcinae 'group 2'

Figure 9

Remarks. This operational group (Figure 9 part, i.e., without the '*Spermophora*' *dieke* group and *Quamtana*) is similar to 'group 1' in that it is composed entirely of six-eyed species. It is weakly supported, indicating that the exact placement of its two clades among other Pholcinae remains dubious. The two clades, however, both receive high to full support in all analyses. The first clade unites the African genera *Anansus* Huber, 2007 and *Nyikoa* Huber, 2007 with the Madagascan genus *Zatavua* Huber, 2003. In a cladistic analysis of morphological characters (Huber 2007), the group was also recovered (even though as paraphyletic) when using successive character weighting (but not when using equal character weights). The character supporting this close relationship was the proximal cheliceral apophyses that point backwards in *Anansus* just as in *Nyikoa* and *Zatavua* (Huber 2007). The idea that these genera might be 'basal' in Pholcinae, i.e., sister to all other Pholcinae (Huber 2003a, 2007) is not supported by our analyses, but considering the low support values at deeper nodes within the subfamily it is neither strongly contradicted.

The second clade is the New World genus *Metagonia*. The genus is species-rich (currently 85 species) and ranges from Argentina to Mexico. The monophyly of the genus has never been seriously contested, and its position among the otherwise almost exclusively Old World Pholcinae has been strongly supported before, both using morphology (Huber 2000) and molecules (Bruvo-Mađarić et al. 2005, Dimitrov et al. 2013). Our analyses include 30 species of *Metagonia*, and provide for the first time a

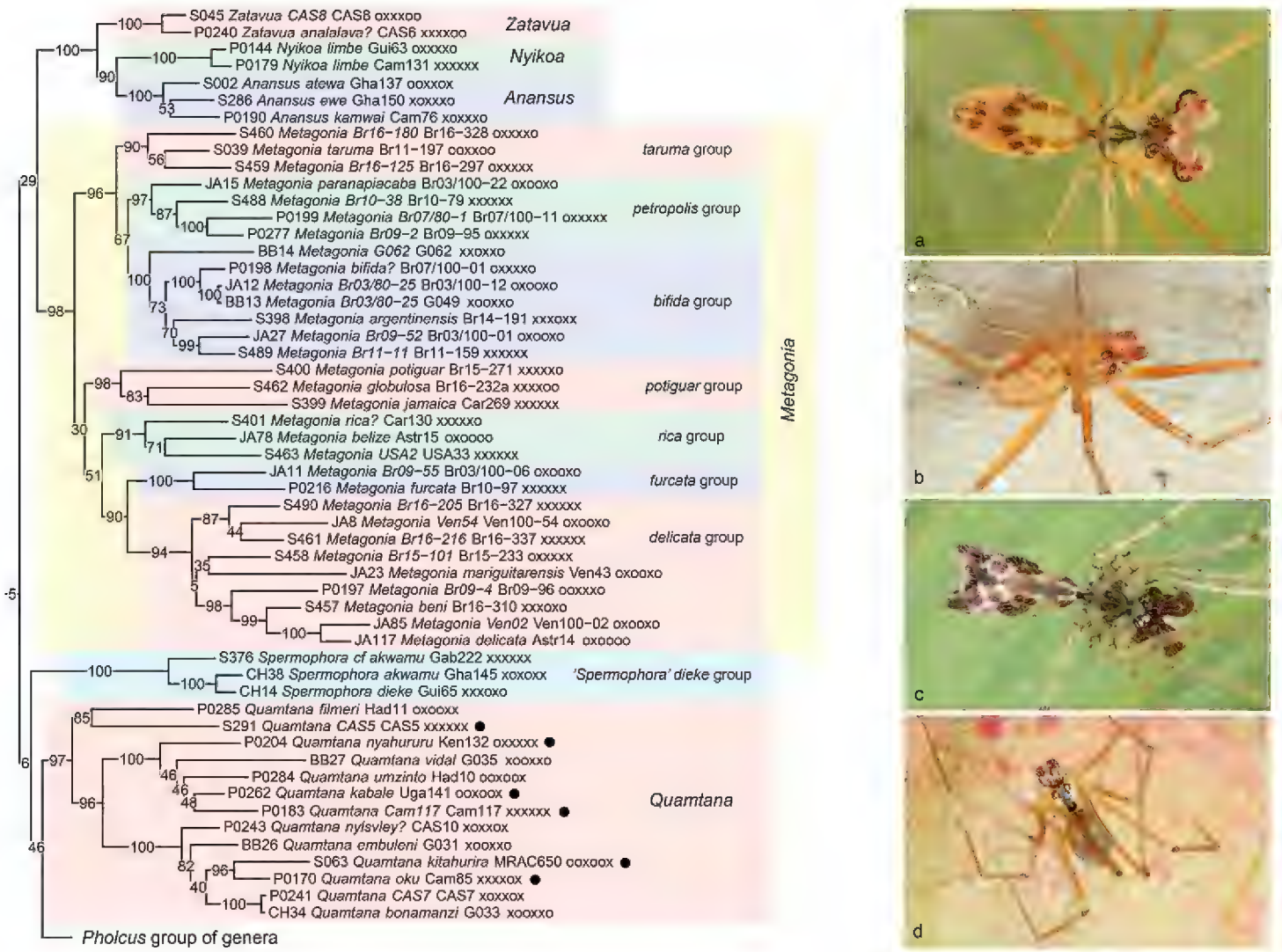

S045 Zatavua CAS8 CAS8 oxxxoo
P0240 Zatavua analalava? CAS6 xxxxoo
Zatavua
P0144 Nyikoa limbe Gui63 oxxxxo
P0179 Nyikoa limbe Cam131 xxxxxx
Nyikoa
S002 Anansus atewa Gha137 ooxxox
S286 Anansus ewe Gha150 xoxxxo
P0190 Anansus kamwai Cam76 xoxxxo
Anansus
S460 Metagonia Br16-180 Br16-328 oxxxxo
S039 Metagonia taruma Br11-197 ooxxoo
S459 Metagonia Br16-125 Br16-297 oxxxxx
taruma group
JA15 Metagonia paranapiacaba Br03/100-22 oxooxo
S488 Metagonia Br10-38 Br10-79 xxxxxx
P0199 Metagonia Br07/80-1 Br07/100-11 oxxxxx
P0277 Metagonia Br09-2 Br09-95 oxxxxx
petropolis group
BB14 Metagonia G062 G062 xxoxxo
P0198 Metagonia bifida? Br07/100-01 oxxxxo
JA12 Metagonia Br03/80-25 Br03/100-12 oxooxo
BB13 Metagonia Br03/80-25 G049 xooxxo
S398 Metagonia argentinensis Br14-191 xxxxxx
JA27 Metagonia Br09-52 Br03/100-01 oxooxo
S489 Metagonia Br11-11 Br11-159 xxxxxx
bifida group
S400 Metagonia potiguar Br15-271 xxxxxo
S462 Metagonia globulosa Br16-232a xxxxoo
S399 Metagonia jamaica Car269 xxxxxx
potiguar group
S401 Metagonia rica? Car130 xxxxxo
JA78 Metagonia belize Astr15 oxoooo
S463 Metagonia USA2 USA33 xxxxxx
rica group
JA11 Metagonia Br09-55 Br03/100-06 oxooxo
P0216 Metagonia furcata Br10-97 xxxxxx
furcata group
S490 Metagonia Br16-205 Br16-327 xxxxxx
JA8 Metagonia Ven54 Ven100-54 oxooxo
S461 Metagonia Br16-216 Br16-337 xxxxxx
S458 Metagonia Br15-101 Br15-233 oxxxxx
JA23 Metagonia mariguitarensis Ven43 oxooxo
P0197 Metagonia Br09-4 Br09-96 ooxxxo
S457 Metagonia beni Br16-310 xxxxxo
JA85 Metagonia Ven02 Ven100-02 oxooxo
JA117 Metagonia delicata Astr14 oxoooo
delicata group
Metagonia
S376 Spermophora cf akwamu Gab222 xxxxxx
CH38 Spermophora akwamu Gha145 xoxxxx
CH14 Spermophora dieke Gui65 xxxxxo
'Spermophora' dieke group
P0285 Quamtana filmeri Had11 oxooxx
S291 Quamtana CAS5 CAS5 xxxxxx ●
P0204 Quamtana nyahururu Ken132 oxxxxx ●
BB27 Quamtana vidal G035 xooxxo
P0284 Quamtana umzinto Had10 ooxoox
P0262 Quamtana kabale Uga141 ooxoox ●
P0183 Quamtana Cam117 Cam117 xxxxxx ●
P0243 Quamtana nyisvley? CAS10 xoxxxo
BB26 Quamtana embuleni G031 xooxxo
S063 Quamtana kitahurira MRAC650 ooxoox ●
P0170 Quamtana oku Cam85 xxxxxo ●
P0241 Quamtana CAS7 CAS7 xoxxxo
CH34 Quamtana bonamanzi G033 xooxxo
Quamtana
Pholcus group of genera
a
b
c
d

Figure 9. Pholcinae 'group 2' (*Zatavua* and relatives, *Metagonia*), and *Quamtana* (marked: non-South African species). Photos **a** *Metagonia taruma* (Brazil) **b** *Metagonia* sp. n. "Br07-1" (Brazil) **c** *Metagonia bifida*? (Brazil) **d** *Quamtana* sp. n. (cf. *mabusai*) (Germany).

test of the operational species groups proposed in Huber (2000: 54–55). Even though those groups were not based on formal cladistic analysis (such an analysis has not yet been performed for *Metagonia*) but on overall and specific similarities, all of them appear mostly or entirely congruent with the present analyses (the only exception is the single aberrant *M. globulosa*). They are listed here in the sequence in which they appear in Figure 9, with newly proposed informal names. (1) *taruma* group (group "3" in Huber 2000); a South American group that is here resolved as monophyletic and not as a paraphyletic 'basal' group as speculated before (Huber 2000); (2) *petropolis* group (no species was known in 2000); a group of litter-dwelling species restricted to the Brazilian Atlantic Forest (Huber et al. 2005b); (3) *bifida* group (group "1" in Huber 2000); this South American group includes the type species *M. bifida* Simon, 1893; all species included share a sclerotized epigynum and (except for the 'basal' undescribed species "G062") a distinctively bifid abdomen; (4) *potiguar* group (not recognized in Huber 2000); this group includes cave dwelling species in Brazil (*M. potiguar* Ferreira et al. 2011) and Jamaica (*M. jamaica* Gertsch, 1986) and the aberrant litter-dwelling *M. globulosa* Huber, 2000 (which was misplaced in group "5" in Huber 2000); *rica* group (group "4" in Huber 2000); a mainly North and Central American

group, possibly ranging into South America, but not including all Caribbean and Central American species as speculated previously (Huber 2000; see previous group); (5) *furcata* group (group "5" in Huber 2000, together with *M. globulosa*); includes only *M. furcata* Huber, 2000 and the undescribed species "Br09-55"; as suspected previously (Huber 2000), it is close to (sister of) the next group; (6) *delicata* group (group "2" in Huber 2000); this group is composed of very small species and ranges from Mexico to northern Argentina.

Pholcinae 'group 3'
Figs 9–12

Remarks. A sister-group relationship between the African genus *Quamtana* and the *Pholcus* group of genera (Figure 9) is recovered in all our analyses. Support values are low, but a morphological cladistic analysis has partly suggested the same relationship (based on a distinct sclerite connecting the genital bulb to the palpal tarsus; Huber 2003c). The monophyly of *Quamtana* is highly supported in all analyses (except for the 4+ genes analysis). It was also supported by morphological data when using character weighting (but not in the equal weights analysis; Huber 2003c).

Within *Quamtana* (Figure 9), our data suggest that there is no simple geographic pattern with respect to South African species (the large majority) versus species from other parts of Africa (marked in Figure 9). By contrast, three species groups with reasonable to full support include species from both South Africa and other regions: the South African *Q. filmeri* Huber, 2003 is sister to the Madagascan undescribed species "CAS5"; the South African *Q. vidal* Huber, 2003 and *Q. umzinto* Huber, 2003 are placed in a group with species from East and Central Africa (*Q. kabale* Huber, 2003, "Cam117"); and the group including the South African *Q. embuleni* Huber, 2003 and *Q. bonamanzi* Huber, 2003 also includes species from East and Central Africa (*Q. kitahurira* Huber, 2003, *Q. oku* Huber, 2003). We suspect that *Quamtana* was once widely distributed throughout Africa but largely replaced by more modern taxa in humid regions and extinguished in northern Africa. The Paris amber fossil *Quamtana huberi* Penney, 2007 supports this view, but its generic assignment is uncertain (Penney 2007).

All remaining clades together (Figs 10–12) represent the *Pholcus* group of genera *sensu* Huber (2011a). This clade was first proposed in Huber & Fleckenstein (2009) based on the distinctive simplified shape of the tarsus IV comb-hairs, and later supported in a cladistic morphological analysis by an additional character (female epigynal 'knob') (Huber 2011a). All our analyses fully support this clade. The previous morphological analysis (Huber 2011a) identified two major problems within this clade: (1) relationships among genera were basically unresolved, resulting in large polytomies; and (2) several species groups assigned to *Pholcus* appeared more closely related to other genera. The present analysis strongly supports the polyphyly of *Pholcus* in its previous composition, and it provides for the first time a reasonable framework to redefine generic limits in this large group (currently 501 species).

The first major clade within the *Pholcus* group of genera (Figure 10) is composed of three Southeast Asian genera (*Calapnita*, *Panjange*, *Uthina* Simon, 1893) as well as several Southeast Asian and Sri Lankan species groups that were originally tentatively assigned to *Pholcus* (Huber 2011a; Huber et al. 2016a, 2016b, Huber and Dimitrov 2014). We informally call it the '*Calapnita-Panjange* clade' because many species in this group are leaf-dwellers, and representatives of *Calapnita* and *Panjange* are particularly strongly adapted to life on green leaves. Remarkably, even some of the species collected in the leaf litter (under large dead leaves on the ground) look like leaf-dwellers rather than litter dwellers (i.e., they have long abdomens, long legs, light colouration; e.g., *Kintaqa satun* (Huber, 2011) and *K. schwendingeri* (Huber, 2011); and Malaysian representatives of *Tissahamia*, previously the *Pholcus ethagala* group). Ancestral character state reconstruction suggests that the ancestor of the entire clade was leaf-dwelling (Eberle et al. 2018).

The present analyses reject the monophyly of *Calapnita* (Figure 10). A recent cladistic analysis of morphological data (Huber 2017) resolved *Calapnita* as monophyletic but with low support (< 50 using Jackknifing). On the other hand, support for the two subgroups, previously called *phyllicola* group and *vermiformis* group, is full in all analyses. The two species groups have been identified long ago (Deeleman-Reinhold 1986b), and have been supported by cladistic analysis (Huber 2017). Our analyses strongly suggest that the *vermiformis* group is closer to species previously in *Pholcus* than to the *phyllicola* group (see below). The *phyllicola* group is thus elevated to genus rank (*Nipisa*; see Taxonomy section below).

Within *Nipisa* (Figure 10), the internal relationships proposed previously (Huber 2017) are mostly supported even though data gaps are severe in this genus (several species with only two genes): (1) *N. lehi* (Huber, 2017) [but not *N. kubah* (Huber, 2017)] is a 'basal' species, i.e., sister to all other species (reasonable to high support); (2) a clade including the species with egg-sacs that have all eggs aligned in a single row (weak support, possibly because *N. kubah* is included, which is contradicted by morphology and egg-sac shape); (3) a clade including *N. semengoh* (Huber, 2011) and its sister group, characterized by the position of the tarsal organ on a turret, a serrate embolus, and the shape of the pore-plates (full support).

The relationships within 'true' *Calapnita* (previously *vermiformis* group) proposed in Huber (2017) are only partly supported: (1) a clade with a continuous connection between epigynal plate and 'knob' (all species in the present analysis except *C. bario* Huber, 2017 and *C. saluang* Huber, 2011; high support); (2) within the previous clade, a clade characterized by a prolateral process at the tip of the procursus (in the present analysis: *C. nunezae* Huber, 2017 and *C. dinagat* Huber, 2017; full support).

The present analyses also reject the monophyly of *Panjange* (Figure 10). They split the genus into two unrelated lineages, one of which is equivalent to what was previously called the *nigrifrons* group; the other is equivalent to the previous *vermiformis* + *cavicola* groups (Deeleman-Reinhold and Platnick 1986, Huber and Nuñeza 2015). Our analyses place each group with reasonable to full support in clades together with species previously assigned to *Pholcus*. A morphological cladistic analysis has recently

supported the monophyly of *Panjange* based on the presence of parallel ridges ventrally on the procursus and on the reduction of the bulbal uncus (Huber and Nuñeza 2015). However, the monophyly was lost when using specific weighting parameters (implied weighting with K = 1 and K = 2), and some morphological characters do in fact support the split of *Panjange*: (1) the loss of distal cheliceral apophyses in 'true' *Panjange* and its closest relatives according to the present analyses; (2) the loss of an uncus in 'true' *Panjange* and its closest relatives according to the present analyses. The *nigrifrons* group is thus elevated to genus rank (*Apokayana*; see Taxonomy section below).

Apokayana is recovered with full support. This is remarkable considering the fact that in the morphological analysis its equivalent (the *Panjange nigrifrons* group) was supported by a single homoplastic character only (Huber and Nuñeza 2015). Within the genus, our analyses identify two subgroups with full support each. These groups do not correspond to the relationships suggested in Huber and Nuñeza (2015). In that analysis, each node was based on a single character, some of them not particularly convincing. We thus tend to prefer the present grouping even though our matrix is particularly incomplete in this genus (we did not manage to get 28S and CO1 sequences for any of the six species included).

The monophyly of 'true' *Panjange* (*vermiformis* + *cavicola* groups) is supported by several morphological characters (Huber and Nuñeza 2015), and receives high support in our present analyses (except for the 4+ genes analysis). The *cavicola* group (including also the two undescribed species "Ind103" and "Ind109") was recovered as paraphyletic in Huber and Nuñeza (2015) but is here resolved as monophyletic. By contrast, the *lanthana* group which was supported by two morphological characters, one of them considered particularly strong (the unique direction of the embolus, pointing in the opposite direction of the appendix) is resolved as monophyletic only in the RogueNaRok tree; in the IQ-TREE and RAxML trees it is paraphyletic with respect to the *cavicola* group (actually, these trees suggest a basal trichotomy). Within the *lanthana* group, three species (*P. malagos* Huber, 2015; *P. casaroro* Huber, 2015; *P. camiguin* Huber, 2015) share asymmetric male pedipalps, a character that is extremely rare in spiders (Huber et al. 2007, Huber and Nuñeza 2015). This group is not recovered in any of the present analyses, where it consistently includes the symmetric *P. lanthana* Deeleman-Reinhold & Deeleman, 1983 (requiring a regain of symmetry or two origins of asymmetry). Only the sister group relationship between *P. dinagat* Huber, 2015 and *P. marilog* Huber, 2015 is strongly supported by both morphology and molecules. In conclusion, alternative topologies within the *lanthana* group are supported by seemingly strong molecular and morphological data, respectively.

Ten species groups previously assigned to *Pholcus* (in Huber 2011a, Huber et al. 2016a, 2016b) are representatives of the '*Calapnita-Panjange* clade' (Figure 10). Of these, nine are entirely Southeast Asian; only the *ethagala* group (now *Tissahamia*) has representatives in Southeast Asia and Sri Lanka. For some of these species groups, our data provide strong evidence about the sister-group or close relatives. All of these groups are here transferred from *Pholcus* to new genera (see Taxonomy section below).

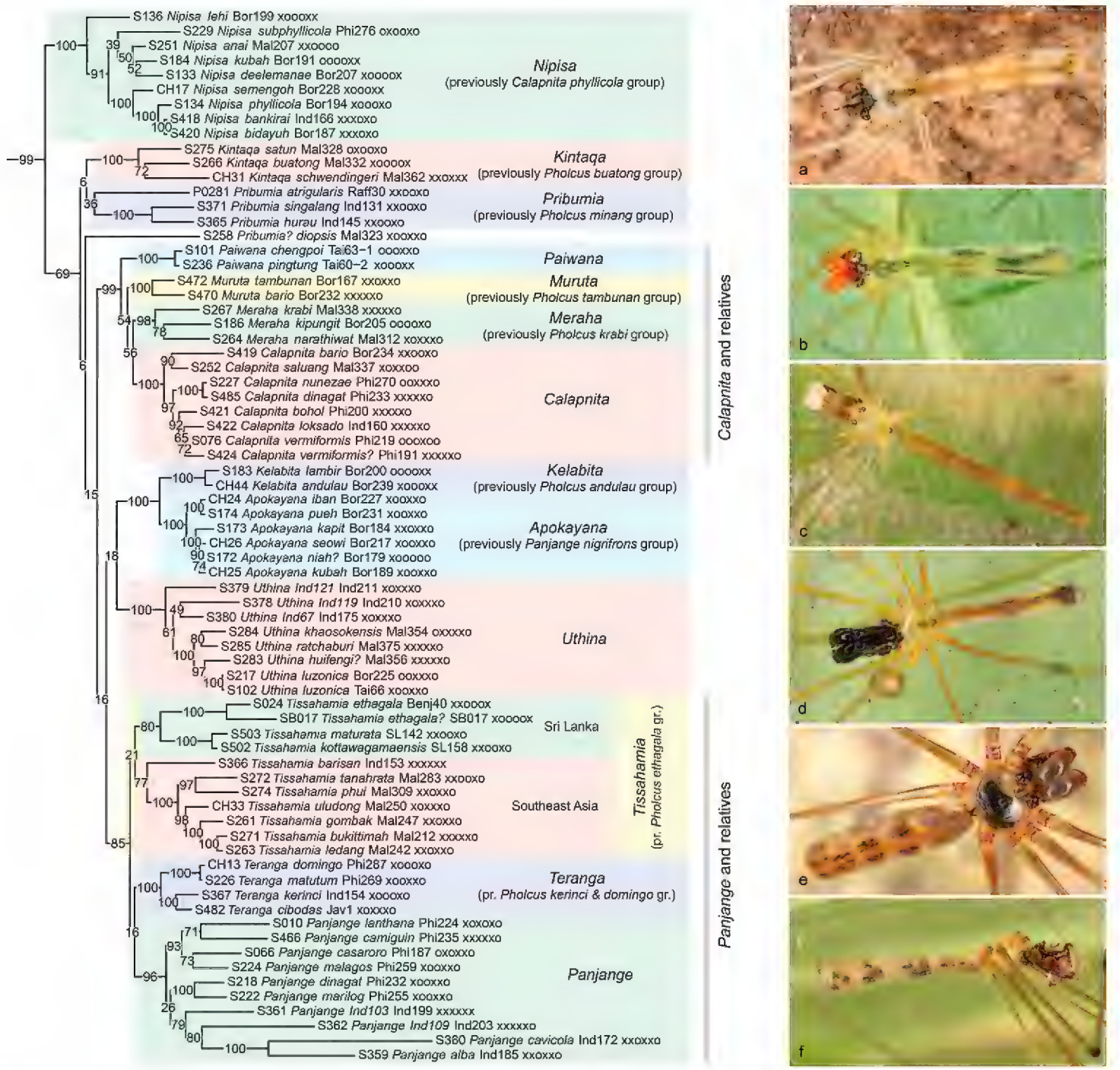

S136 Nipisa lehi Bor199 xoooxx
S229 Nipisa subphyllicola Phi276 oxooxo
S251 Nipisa anai Mal207 xxoooo
S184 Nipisa kubah Bor191 oooxxx
S133 Nipisa deelemanae Bor207 xoooox
CH17 Nipisa semengoh Bor228 xoooxx
S134 Nipisa phyllicola Bor194 xoooxo
S418 Nipisa bankirai Ind166 xxxxxo
S420 Nipisa bidayuh Bor187 xxxxxo
Nipisa
(previously Calapnita phyllicola group)
S275 Kintaqa satun Mal328 oxooxo
S266 Kintaqa buatong Mal332 xoooox
CH31 Kintaqa schwendingeri Mal362 xxoxxx
Kintaqa
(previously Pholcus buatong group)
P0281 Pribumia atrigularis Raff30 xxoxxo
S371 Pribumia singalang Ind131 xxooxo
S365 Pribumia hurau Ind145 xxooxo
Pribumia
(previously Pholcus minang group)
S258 Pribumia? diopsis Mal323 xooxxo
S101 Paiwana chengpoi Tai63–1 oooxxo
S236 Paiwana pingtung Tai60–2 xoooxx
Paiwana
S472 Muruta tambunan Bor167 xxoxxo
S470 Muruta bario Bor232 xxxxxo
Muruta
(previously Pholcus tambunan group)
S267 Meraha krabi Mal338 xxxxxo
S186 Meraha kipungit Bor205 oooxxo
S264 Meraha narathiwat Mal312 xoxxxo
Meraha
(previously Pholcus krabi group)
S419 Calapnita bario Bor234 xxooxo
S252 Calapnita saluang Mal337 xoxxoo
S227 Calapnita nunezae Phi270 ooxxxo
S485 Calapnita dinagat Phi233 xxxxxo
S421 Calapnita bohol Phi200 xxxxxo
S422 Calapnita loksado Ind160 xxxxxo
S076 Calapnita vermiformis Phi219 ooxxoo
S424 Calapnita vermiformis? Phi191 xxxxxo
Calapnita
S183 Kelabita lambir Bor200 oooxxx
CH44 Kelabita andulau Bor239 xoooxx
Kelabita
(previously Pholcus andulau group)
CH24 Apokayana iban Bor227 xooxxo
S174 Apokayana pueh Bor231 xooxxo
S173 Apokayana kapit Bor184 xxoxxo
CH26 Apokayana seowi Bor217 xooxxo
S172 Apokayana niah? Bor179 xooooo
CH25 Apokayana kubah Bor189 xooxxo
Apokayana
(previously Panjange nigrifrons group)
S379 Uthina Ind121 Ind211 xoxxxo
S378 Uthina Ind119 Ind210 xoxxxo
S380 Uthina Ind67 Ind175 xoxxxo
S284 Uthina khaosokensis Mal354 oxxxxo
S285 Uthina ratchaburi Mal375 xxxxxo
S283 Uthina huifengi? Mal356 xxxxxo
S217 Uthina luzonica Bor225 ooxxxo
S102 Uthina luzonica Tai66 xooxxo
Uthina
Calapnita and relatives
S024 Tissahamia ethagala Benj40 xxooox
SB017 Tissahamia ethagala? SB017 xoooox
Sri Lanka
S503 Tissahamia maturata SL142 xxooxo
S502 Tissahamia kottawagamaensis SL158 xxooxo
S366 Tissahamia barisan Ind153 xxxxxx
S272 Tissahamia tanahrata Mal283 xxooxo
S274 Tissahamia phui Mal309 xxoxxo
CH33 Tissahamia uludong Mal250 xoxxxo
Southeast Asia
S261 Tissahamia gombak Mal247 xxoxxo
S271 Tissahamia bukittimah Mal212 xxxxxo
S263 Tissahamia ledang Mal242 xxoxxo
Tissahamia
(pr. Pholcus ethagala gr.)
CH13 Teranga domingo Phi287 xoooxo
S226 Teranga matutum Phi269 xooxxo
S367 Teranga kerinci Ind154 xoooxo
S482 Teranga cibodas Jav1 xoxxxo
Teranga
(pr. Pholcus kerinci & domingo gr.)
S010 Panjange lanthana Phi224 xoxoxo
S466 Panjange camiguin Phi235 xxxxxo
S066 Panjange casaroro Phi187 oxoxxo
S224 Panjange malagos Phi259 xooxxo
S218 Panjange dinagat Phi232 xooxxo
S222 Panjange marilog Phi255 xooxxo
S361 Panjange Ind103 Ind199 xxxxxx
S362 Panjange Ind109 Ind203 xxxxxo
S360 Panjange cavicola Ind172 xxoxxo
S359 Panjange alba Ind185 xxoxxo
Panjange
Panjange and relatives
a
b
c
d
e
f

Figure 10. *Calapnita-Panjange* clade **a** *Kintaqa satun* (Malaysia) **b** *Meraha narathiwat* (Thailand) **c** *Calapnita vermiformis* (Philippines) **d** *Apokayana kapit* (Sarawak) **e** *Uthina* sp. n. "Ind121" (Indonesia) **f** *Panjange casaroro* (Philippines).

A sister-group relationship between *Kelabita* (previously the *Pholcus andulau* group) and *Apokayana* (previously the *Panjange nigrifrons* group) is fully supported in all our analyses (except for the 4+ genes tree where *Kelabita* is not represented). Both genera are restricted to Borneo and share habitus, colouration, web structure, and microhabitat (Huber and Leh Moi Ung 2016, Huber et al. 2016a).

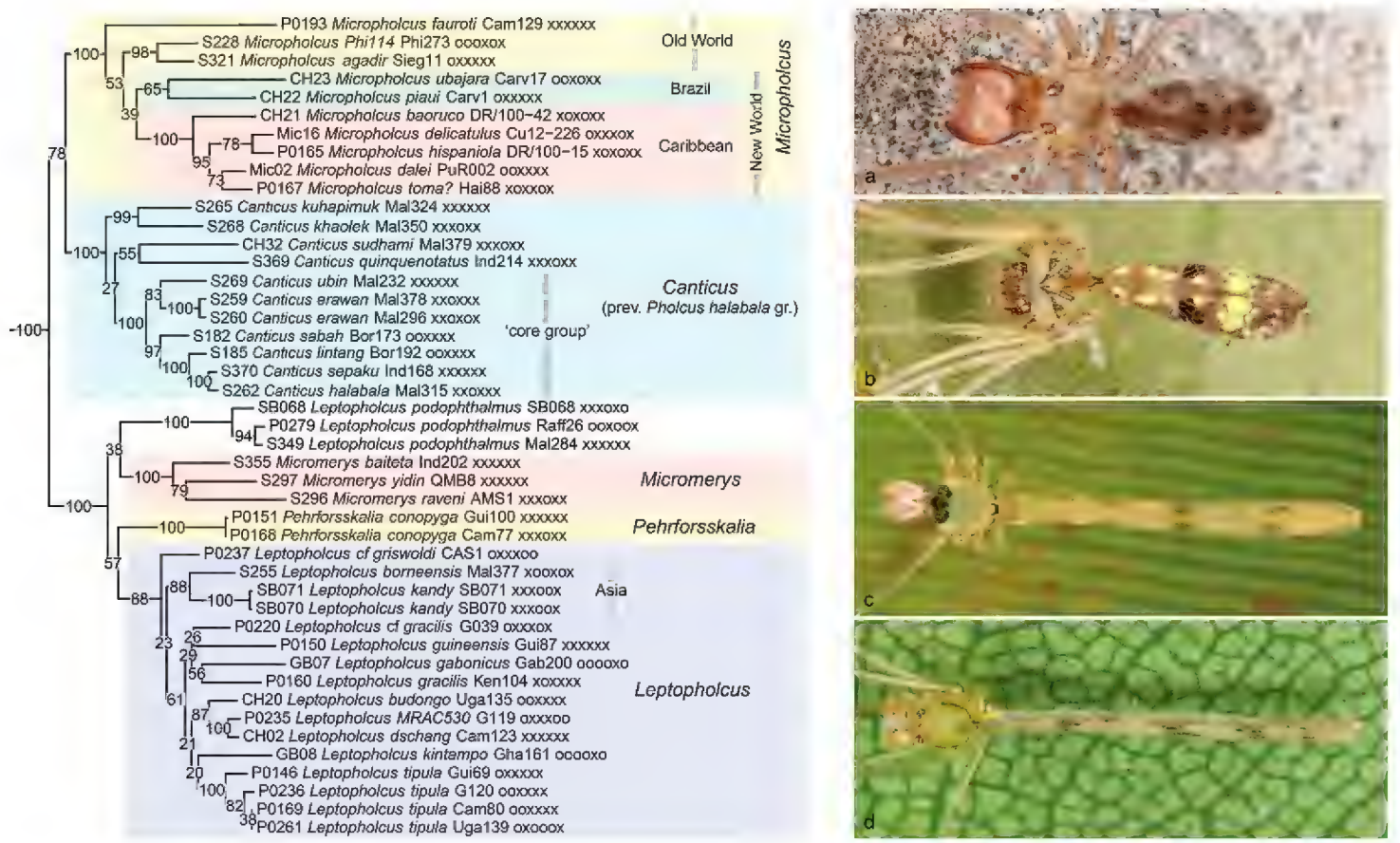
The western Indonesian '*Pholcus kerinci* group' (Huber 2011a) and the Philippine '*Pholcus domingo* group' (Huber et al. 2016b) are both fully supported, as is their sister-group relationship (Figure 10). They are joined in the new genus *Teranga* (see Taxonomy section below). Together with *Tissahamia* (previously the *Pholcus ethagala* group) and with 'true' *Panjange* they form a clade that is recovered in all analyses with reasonable support. This clade was supported in almost exactly the same composition by morphological cladistic analysis (Huber 2011a) except that the '*Panjange*' *nigrifrons*

group was also included (the '*Pholcus domingo* group' was not yet known in 2011). The clade is supported by the loss of the bulbal uncus and by the loss of distal male cheliceral apophyses [in Huber 2011a, the latter character supports a more inclusive taxon (including *Leptopholcus* Simon, 1893) that is strongly rejected by the present molecular data]. *Tissahamia* consists of two subgroups, a Sri Lankan subgroup and a Southeast Asian (Malaysian Peninsula, Sumatra) subgroup. The subgroups are consistently recovered in all our analyses with modest to reasonable support, but the monophyly of the entire group is only recovered in the IQ-TREE analysis (low support). Morphological analysis recovered the group, but with varying support depending on weighting regime (Huber 2011a).

Three genera composed of species that were previously assigned to *Pholcus* are consistently placed in a highly supported clade together with 'true' *Calapnita* (Figure 10): *Paiwana* (previously not assigned to a group), *Muruta* (previously the *Pholcus tambunan* group; Huber et al. 2016b), and *Meraha* (previously the *Pholcus krabi* group; Huber et al. 2016b). We know of no convincing morphological synapomorphy for this group but note two interesting similarities: representatives of 'true' *Calapnita* and of *Meraha* share the loss of piriform gland spigots on the anterior lateral spinnerets (Huber 2011a, 2017, Huber et al. 2016b); representatives of 'true' *Calapnita* and of *Muruta* and *Paiwana* share the distinctive shape of the epigynum (roughly triangular, with 'knob' directed towards anterior; Huber et al. 2016b, Huber 2017; Huber and Dimitrov 2014).

For two further genera composed of species previously assigned to *Pholcus* the present analysis supports the monophyly but gives not clear indication about their closest relatives within the '*Calapnita-Panjange* clade' (Figure 10): *Pribumia* (previously the *Pholcus minang* group; Huber 2011a) and *Kintaqa* (previously the *Pholcus buatong* group; Huber et al. 2016a). All analyses except the IQ-TREE analysis place *Kintaqa* as sister to *Uthina*, but with low support. We know of no potential morphological synapomorphy that links these two groups. *Pribumia* is in our analysis represented by four species. Of these, *P. diopsis* (Simon, 1901) is never placed within the group; together with *P. atrigularis* (Simon, 1901) it is detected as a rogue taxon and excluded in the RogueNaRok tree. External relationships of *Pribumia* remain dubious. The hypothesis that the genus might be close to *Tissahamia* (previously the '*Pholcus ethagala* group'; Huber 2011a) is supported by numerous distinctive morphological similarities but it is not supported by the present data. However, note that in our analysis *Pribumia* suffers seriously from missing data (we were not able to sequence 28S for any of the four species).

The second major clade within the *Pholcus* group of genera (Figure 11) is composed of four 'old' genera (*Micropholcus*; *Leptopholcus*; *Micromerys* Bradley, 1877; *Pehrforsskalia* Deeleman-Reinhold & van Harten, 2001) and *Cantikus* (previously the *Pholcus halabala* group; Huber 2011a, Huber et al. 2016a). Except for one clade of Neotropical *Micropholcus*, all representatives are Old World taxa. We informally call it the '*Micropholcus-Leptopholcus* clade'. This clade receives full support in all our analyses, and major internal relationships are also well resolved. Three subclades are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S228 Micropholcus Phi114 Phi273 ooxxox
S321 Micropholcus agadir Sieg11 oxxxxx
CH23 Micropholcus ubajara Carv17 ooxoxx
CH22 Micropholcus piaui Carv1 oxxxxx
CH21 Micropholcus baoruco DR/100–42 xoxoxx
Mic16 Micropholcus delicatulus Cu12–226 oxxxox
P0165 Micropholcus hispaniola DR/100–15 xoxoxx
Mic02 Micropholcus dalei PuR002 ooxxxx
P0167 Micropholcus toma? Hai88 xoxxox
Old World
Brazil
Caribbean
New World
Micropholcus
S265 Canticus kuhapimuk Mal324 xxxxxx
S268 Canticus khaolek Mal350 xxxoxx
CH32 Canticus sudhami Mal379 xxxoxx
S369 Canticus quinquenotatus Ind214 xxxoxx
S269 Canticus ubin Mal232 xxxxxx
S259 Canticus erawan Mal378 xxoxxx
S260 Canticus erawan Mal296 xxoxox
S182 Canticus sabah Bor173 ooxxxx
S185 Canticus lintang Bor192 ooxxxx
S370 Canticus sepaku Ind168 xxxxxx
S262 Canticus halabala Mal315 xxoxxx
'core group'
Canticus
(prev. Pholcus halabala gr.)
SB068 Leptopholcus podophthalmus SB068 xxxoxo
P0279 Leptopholcus podophthalmus Raff26 ooxoox
S349 Leptopholcus podophthalmus Mal284 xxxxxx
S355 Micromerys baiteta Ind202 xxxxxx
S297 Micromerys yidin QMB8 xxxxxx
S296 Micromerys raveni AMS1 xxxoxx
Micromerys
P0151 Pehrforsskalia conopyga Gui100 xxxxxx
P0168 Pehrforsskalia conopyga Cam77 xxxoxx
Pehrforsskalia
P0237 Leptopholcus cf griswoldi CAS1 oxxxoo
S255 Leptopholcus borneensis Mal377 xooxox
SB071 Leptopholcus kandy SB071 xxxoox
SB070 Leptopholcus kandy SB070 xxxoox
Asia
P0220 Leptopholcus cf gracilis G039 oxxxox
P0150 Leptopholcus guineensis Gui87 xxxxxx
GB07 Leptopholcus gabonicus Gab200 oooxxo
P0160 Leptopholcus gracilis Ken104 xoxxxx
CH20 Leptopholcus budongo Uga135 ooxxxx
P0235 Leptopholcus MRAC530 G119 oxxxoo
CH02 Leptopholcus dschang Cam123 xxxxxx
GB08 Leptopholcus kintampo Gha161 oooxxo
P0146 Leptopholcus tipula Gui69 oxxxxx
P0236 Leptopholcus tipula G120 ooxxxx
P0169 Leptopholcus tipula Cam80 ooxxxx
P0261 Leptopholcus tipula Uga139 oxoxox
Leptopholcus
a
b
c
d

Figure 11. *Micropholcus-Leptopholcus* clade **a** *Micropholcus* sp. n. "Br15-152" (Brazil) **b** *Canticus sepaku* (East Kalimantan) **c** *Micromerys baiteta* (West Papua) **d** *Leptopholcus borneensis* (Singapore).

fully supported each: *Micropholcus*; *Cantikus*; and a subclade including *Leptopholcus*, *Micromerys*, and *Pehrforsskalia*. All analyses put *Micropholcus* as sister to *Cantikus*, but with modest support.

Micropholcus is ecologically diverse, including ground-dwelling as well as rock- and leaf-dwelling species, and together with *Pholcus* it is also the only genus with autochthonous species in both the New and Old World. Our analysis rejects the previous idea that *Micropholcus* is 'basal' in the *Pholcus* group of genera (i.e., in a basal trichotomy, with *Sihala* occupying the second branch and all other taxa the third branch; Huber 2011a). Within *Micropholcus*, our analyses all support a monophyletic New World clade, but with low support values (reasonable support in the 4+ genes analysis). Within the New World clade, a Caribbean clade is fully supported. A remarkable sister-group relationship that is highly supported by the present data is between the Moroccan '*Pholcus' agadir* (now transferred to *Micropholcus*; see Taxonomy section below) and the undescribed Philippine species "Phi114". Both have very limited distributions; only one further species of *Micropholcus* (other than the pantropical *M. fauroti*) is known from between Morocco and the Philippines: *M. jacominae* Deeleman-Reinhold & van Harten, 2001 from Yemen. We suspect that *Micropholcus* in the Old World has a relict distribution, just as it has been hypothesized for South American *Micropholcus* (Huber et al. 2005a, 2014).

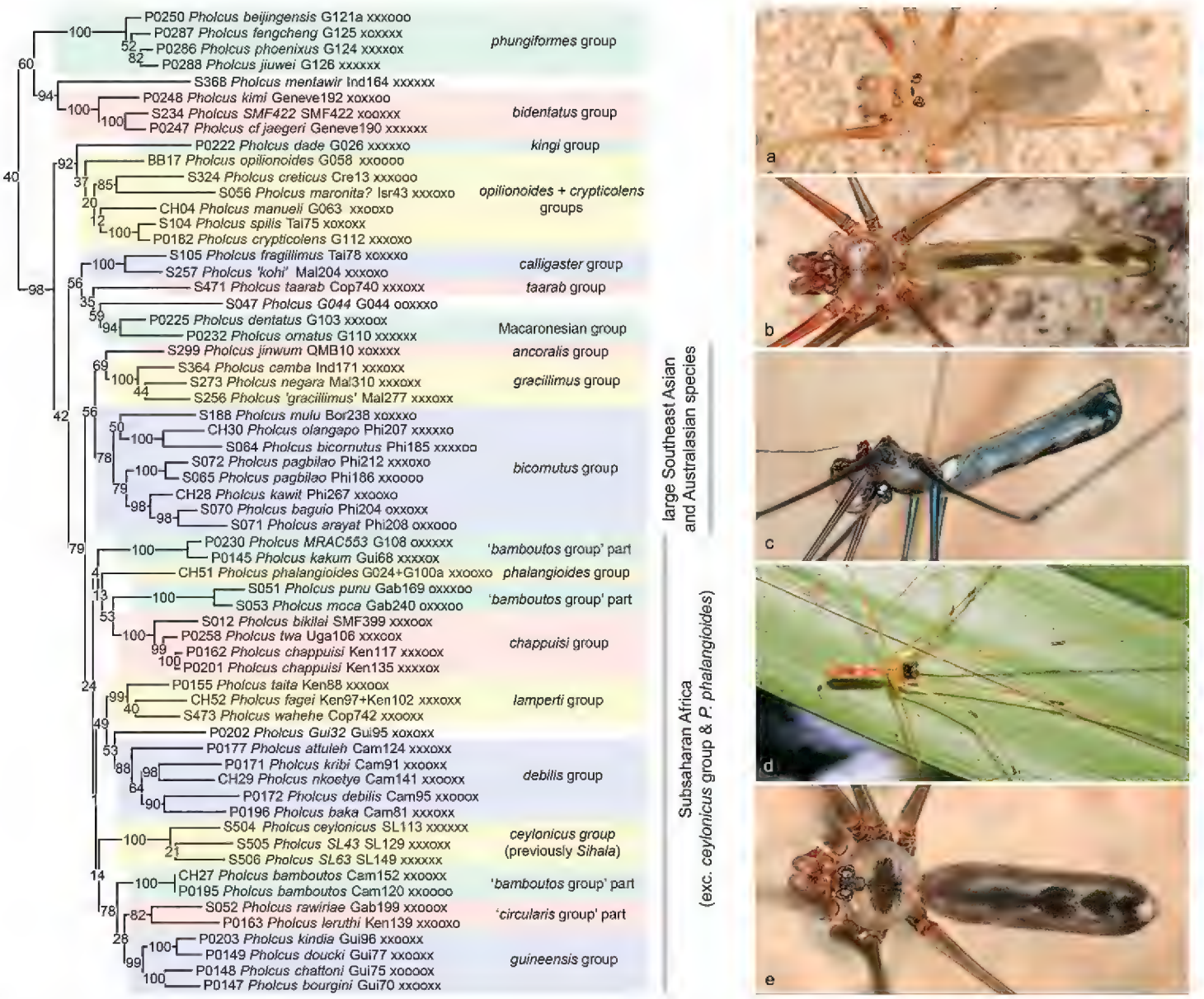
Cantikus was recently revised (as '*Pholcus' halabala* group; Huber et al. 2016a) and divided into a 'core group' that was supported by numerous morphological and behavioral similarities, and a group of species that were assigned to the group tentatively.

This tentative assignment was based mainly on preliminary results from the present molecular analysis; a putative morphological synapomorphy for the entire genus *Cantikus* was and is not known. The present analyses fully support both the entire genus and the core group; the genus includes *C. quinquenotatus* (Thorell, 1878), making the *quinquenotatus* group proposed in Huber (2011a) obsolete; and it highly to fully supports the sister group relationship between the two rock-dwelling species *C. kuhapimuk* Huber, 2016 and *C. khaolek* Huber, 2016.

The clade including *Leptopholcus*, *Micromerys*, and *Pehrforsskalia* (Figure 11) was only partly supported in a previous cladistic analysis of morphological data (Huber 2011a): while *Leptopholcus* and *Micromerys* were consistently seen as sister taxa (with a mono- or paraphyletic *Leptopholcus*), the position of *Pehrforsskalia* varied widely. The characters supporting a close relationship among the three genera are the distal position of the lateral apophyses on the male chelicerae, and the absence of frontal cheliceral apophyses (Huber 2011a). The present analyses fully support this clade. Within the clade, 'basal' relationships are unresolved, essentially resulting in a tetrachotomy: (1) '*Leptopholcus' podophthalmus* (Simon, 1893) is not clearly included in 'true' *Leptopholcus*. (2) The Australasian *Micromerys* receives full support in all analyses. (3) The African *Pehrforsskalia* is only represented by its type species. (4) 'True' *Leptopholcus* receives reasonable to full support and includes both African and Asian representatives but not the Asian *L. podophthalmus* (and its putative close relative *L. tanikawai* Irie, 1999 that is not included in our analyses). Within *Leptopholcus*, our data provide little resolution, but an Asian clade (represented by *L. borneensis* Deeleman-Reinhold, 1986 and *L. kandy* Huber, 2011) receives reasonable support. Among these four clades, *Pehrforsskalia* is the only one that does not share the distinctively serrated tip of the male palpal trochanter apophysis (Huber 2011b), suggesting that it may be sister to the other three clades.

The third and last major clade within the *Pholcus* group of genera is 'true' *Pholcus* (Figure 12). Support for this group is very low in the IQ-TREE analysis, which reflects the fact that one of the two basal subclades (including the *phungiformes* and *bidentatus* groups and *P. mentawir* Huber, 2011) is closer to the *Micropholcus-Leptopholcus* clade than to 'true' *Pholcus* in some analyses (RAxML, RogueNaRok). By contrast, the 4+ genes analysis recovers the monophyly of 'true' *Pholcus* with reasonable support, suggesting that the poor support or non-monophyly of 'true' *Pholcus* in some analyses may result from the many missing data in our full matrix.

Even after removing the eleven species groups that are here placed in the *Calapnita-Panjange* clade and in the *Micropholcus-Leptopholcus* clade, *Pholcus* continues to be the most species rich genus in Pholcidae. It now contains 321 species, most of which are distributed in tropical and subtropical Old World regions. The only exception is the *kingi* group with ten species in the southeastern USA (Huber 2011a). Most species of *Pholcus* resemble the synanthropic type species *P. phalangioides* in being relatively large, long-legged, brown, and in having a cylindrical abdomen; most or all of these species build their webs in large sheltered spaces. However, the genus is ecologically diverse and includes small litter dwellers with relatively short legs, rock- and ground dwellers with oval abdomens, and pale leaf-dwellers with worm-shaped abdomens.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P0287 Pholcus fengcheng G125 xoxxxx
P0286 Pholcus phoenixus G124 xxxxox
P0288 Pholcus jiuwei G126 xxxxxx
phungiformes group
S368 Pholcus mentawir Ind164 xxxxxx
P0248 Pholcus kimi Geneve192 xoxxoo
S234 Pholcus SMF422 SMF422 xooxxx
P0247 Pholcus cf jaegeri Geneve190 xxxxxx
bidentatus group
P0222 Pholcus dade G026 xxxxxo
kingi group
BB17 Pholcus opilionoides G058 xxoooo
S324 Pholcus creticus Cre13 xxxooo
S056 Pholcus maronita? Isr43 xxxoxo
opilionoides + crypticolens groups
CH04 Pholcus manueli G063 xxooxo
S104 Pholcus spilis Tai75 xoxoxx
P0182 Pholcus crypticolens G112 xxxoxo
S105 Pholcus fragillimus Tai78 xoxxxo
calligaster group
S257 Pholcus 'kohi' Mal204 xxxoxo
S471 Pholcus taarab Cop740 xxxoxx
taarab group
S047 Pholcus G044 G044 ooxxxo
P0225 Pholcus dentatus G103 xxxoox
P0232 Pholcus ornatus G110 xxxxxx
Macaronesian group
S299 Pholcus jinwum QMB10 xoxxxx
ancoralis group
S364 Pholcus camba Ind171 xxxoxx
S273 Pholcus negara Mal310 xxxoxx
S256 Pholcus 'gracillimus' Mal277 xxxoxx
gracillimus group
S188 Pholcus mulu Bor238 xoxxxo
CH30 Pholcus olangapo Phi207 xxxxxo
S064 Pholcus bicornutus Phi185 xxxxoo
S072 Pholcus pagbilao Phi212 xxxoxo
S065 Pholcus pagbilao Phi186 xxoooo
CH28 Pholcus kawit Phi267 xxooxo
S070 Pholcus baguio Phi204 oxxoxx
S071 Pholcus arayat Phi208 oxxooo
bicornutus group
P0230 Pholcus MRAC553 G108 oxxxxx
P0145 Pholcus kakum Gui68 xxxxox
'bamboutos group' part
CH51 Pholcus phalangioides G024+G100a xxooxo
phalangioides group
S051 Pholcus punu Gab169 oxxxoo
S053 Pholcus moca Gab240 oxxxoo
'bamboutos group' part
S012 Pholcus bikilai SMF399 xxxoox
P0258 Pholcus twa Uga106 xxxoox
P0162 Pholcus chappuisi Ken117 xxxoox
P0201 Pholcus chappuisi Ken135 xxxxox
chappuisi group
P0155 Pholcus taita Ken88 xxxoox
CH52 Pholcus fagei Ken97+Ken102 xxxoxx
S473 Pholcus wahehe Cop742 xxooxx
lamperti group
P0202 Pholcus Gui32 Gui95 xoxoxx
P0177 Pholcus attuleh Cam124 xxxoxx
P0171 Pholcus kribi Cam91 xxooxx
CH29 Pholcus nkoetye Cam141 xxooxx
P0172 Pholcus debilis Cam95 xxooox
P0196 Pholcus baka Cam81 xxxoxx
debilis group
S504 Pholcus ceylonicus SL113 xxxxxx
S505 Pholcus SL43 SL129 xxxoxx
S506 Pholcus SL63 SL149 xxxxxx
ceylonicus group (previously Sihala)
CH27 Pholcus bamboutos Cam152 xxooxx
P0195 Pholcus bamboutos Cam120 xxoooo
'bamboutos group' part
S052 Pholcus rawiriae Gab199 xxooox
P0163 Pholcus leruthi Ken139 xxooxo
'circularis group' part
P0203 Pholcus kindia Gui96 xxooxx
P0149 Pholcus doucki Gui77 xxooxx
P0148 Pholcus chattoni Gui75 xoooox
P0147 Pholcus bourgini Gui70 xxooxx
guineensis group
large Southeast Asian and Australasian species
Subsaharan Africa (exc. ceylonicus group & P. phalangioides)
a
b
c
d
e

Figure 12. *Pholcus* **a** *P. creticus* (Crete) **b** *P. camba* (Sulawesi) **c** *P. mulu* (Sarawak) **d** *P. baka* (Gabon) **e** *P.* sp. n. "SL43" (Sri Lanka).

In a first effort to structure the known diversity of *Pholcus*, the genus was divided into 29 operational species groups (Huber 2011a), including 25 species groups in the 'core group', i.e., in 'true' *Pholcus*. Even though the aim was to identify monophyla, some groups were explicitly proposed as 'waste baskets groups' (e.g., the *bamboutos* group) or as "probably not monophyletic" (e.g., the *circularis* group). The present analysis clarifies a number of relationships, it supports several of the species groups and rejects others, and it confirms the non-monophyly of some groups as suspected. However, we acknowledge that internal relationships in *Pholcus* remain highly uncertain and need considerably more work. Our data seem to suffer from two main problems that result in variable topologies among different types of analyses: (1) Even though *Pholcus* is in our analyses represented by more species than any other genus (59), our sample is still highly incomplete, including only 18% of the described species and entirely missing seven of the previously suggested species groups (*alticeps*, *nenjukovi*, *ponticus*, *zham*, *yichengicus*, *taishan*, and *nagasakiensis* groups). (2) The percentage of missing sequences is high in *Pholcus*, partly due to the fact that we identified paralogs for 28S and 18S that we excluded, partly due to other unidentified problems.

Of the 25 operational species groups within 'true' *Pholcus* proposed previously (Huber 2011a), ten are supported by the present data: *phungiformes* group, *bidentatus* group, *calligaster* group, Macaronesian group, *gracillimus* group (excl. *P. mentawir*), *bicornutus* group, *chappuisi* group, *lamperti* group, *debilis* group (incl. *P. nkoetye* Huber, 2011 and *P. kribi* Huber, 2011), and *guineensis* group. Four groups are represented by single species (*taarab* group, *ancoralis* group, *phalangioides* group, *kingi* group). Seven groups are missing in the analyses (see above). For the remaining four groups, the present analyses reject the monophyly: (1) The *bamboutos* group is polyphyletic as expected and the six species in our analyses split into four parts; of these *P. kribi* is moved to the *debilis* group; *P. bamboutos* Huber, 2011 is close to the *guineensis* group; the affinities of the other four species are unclear. (2) The *circularis* group is represented by three species; of these, *P. nkoetye* is moved to the *debilis* group; *P. leruthi* Lessert, 1935 and *P. rawiriae* Huber, 2014 are sister species and close to the *guineensis* group. (3/4) The *opilionoides* and *crypticolens* groups are both rejected, but together with the North American *kingi* group they form a monophylum with reasonable to high support (except for the 4+ genes analysis) but with unknown affinities with other groups.

The present analysis identifies two major clades within 'true' *Pholcus* that are remarkable even though support values are low to modest. (1) A clade combining the *ancoralis*, *gracillimus*, and *bicornutus* groups is composed of large dark Southeast Asian and Australasian species; a close relationship between the *ancoralis* group and the *bicornutus* group has been suspected before, based on male ocular area modifications (Huber 2011a: 314). (2) A large clade including all Subsaharan African taxa. This clade has low bootstrap support but SH values range from 81 to 96, so we consider this a first tentative indication that tropical African *Pholcus* might form a large monophylum. The two species that disrupt this picture were both identified as rogue taxa: *P. taarab* Huber, 2011 (which is not included in the clade but is African), and *P. phalangioides* (which is included but is most probably not originally African). On the other hand, the inclusion of the Sri Lankan genus *Sihala* Huber, 2011 in this clade is plausible, even though weakly supported. Our data highly support the inclusion of *Sihala* in 'true' *Pholcus*, but neither morphology nor molecules seem to give an indication about its sister taxon.

Notes on genera not included in the present analyses

Aucana Huber, 2000. This Chilean genus (four species; formally including the mysterious New Caledonian *A. kaala* Huber, 2000) was previously thought to be a member of Ninetinae (Huber 2000, 2011b). However, the procursus (dorsal apophysis and corresponding ventral pocket) suggests a placement in Arteminae. Within Arteminae, it shares an exposed tarsal organ with *Chisosa* and *Nita* (Huber 2000, 2011b).

Blancoa Huber, 2000. A small Venezuelan genus (two species), probably member of Modisiminae (Huber 2000), but the sister group remains entirely obscure.

Canaima Huber, 2000. Also probably member of Modisiminae, with only two species restricted to Trinidad and Venezuela (Huber 2000). The shape of the ventral apo-

physis on the male palpal femur is reminiscent of the Venezuelan clade including *Mecolaesthus*, *Stenosfemuraia*, *Systenita*, and 'true' *Coryssocnemis*.

Cenemus Saaristo, 2001. A small Seychellois genus (three species), member of Smeringopinae; a morphological cladistic analysis (Huber 2012) suggested a placement in the 'northern clade' of Smeringopinae even though the Seychelles are geographically much closer to the 'southern clade'.

Enetea Huber, 2000. A monotypic Bolivian genus, member of Ninetinae (Huber 2000); the sister group remains entirely obscure.

Galapa Huber, 2000. A small genus (two species) restricted to the Galapagos Islands, member of Ninetinae (Huber 2000); the sister group remains entirely obscure.

Ossinissa Dimitrov & Ribera, 2005. A monotypic genus from the Canary Islands, member of the *Pholcus* group of genera (Huber 2011a); the sister group is dubious, but we suspect a close relationship with other Canary Island cavernicole species in 'true' *Pholcus* (*P. baldiosensis* Wunderlich, 1992; *P. corniger* Dimitrov & Ribera, 2006).

Pomboa Huber, 2000. Member of Modisiminae, with currently four species restricted to Colombia. The vertical hairs in high density on the leg tibiae suggest an affinity to *Pisaboa* and *Waunana* (Huber 2000).

Queliceria González-Sponga, 2003. A monotypic Venezuelan genus, probably member of Modisiminae; the sister group remains entirely obscure.

Tibetia Zhang, Zhu & Song, 2006. A monotypic Chinese (Tibetan) genus, probably member of Arteminae; the sister group remains entirely obscure.

Tolteca Huber, 2000. A small Mexican genus (two species), member of Ninetinae. We predict that *Tolteca* is member of the North and Central American & Caribbean clade (Figure 2), together with *Pholcophora* and *Papiamenta*. The frontal humps on the male sternum and the shape of the procursus are reminiscent of *Pholcophora* (Huber 2000).

Taxonomy

The present data suggest a large number of new undescribed genera. Twelve of them are composed entirely of undescribed new species; these will be described separately: three in Ninetinae (in our analyses: "Br15-159", "Om6", Ven01"); two in Arteminae ("Geneve59", "Ind82"–"Ind96"); five in Modisiminae ("Br16-44", MACN270", "Br16-178" + "Br16-50", "Br16-196", "Br15-45"); and two in Pholcinae ("CAS13", "Ind206").

Other new genera will result from splitting of known genera. Of these, several receive high support but taxonomic changes will not be implemented here for various reasons:

(1) taxonomic work on these taxa is currently in progress and the formal taxonomic changes will be published in that context ['*Holocneminus' huangdi*, South American '*Psilochorus*', *Holocnemus caudatus* (Dufour, 1820)].

(2) The included species need to be restudied in order to assess the scope of the new genera and to formulate diagnoses (Central American '*Coryssocnemis*').

Some potentially new genera are suggested by the present data but with low support values and/or without clear support from morphology. We suggest that these cases should be re-evaluated in detail in separate studies.

(1) For the southern clade of *Mesabolivar*, our analyses suggest two options: either to synonymize *Mesabolivar* and *Otavaloa* with *Litoporus* (resulting in a huge, very heterogeneous group), or to split *Mesabolivar*. The latter would preserve the names *Litoporus*, *Mesabolivar*, and *Otavaloa*, and possibly revalidate the name *Kaliana* Huber, 2000 (synonymized with *Mesabolivar* in Astrin et al. 2007), but possibly result in a morphologically non-diagnosable genus for the southern clade of *Mesabolivar*; *Teuia* would be an available name for this group.
(2) The *Smeringopus chogoria* and *rubrotinctus* groups together could either form a new genus, stay in *Smeringopus*, or be moved to *Smeringopina*.
(3) *Leptopholcus podophthalmus* (and its close relative *L. tanikawai*) may or may not represent a separate genus.

For *Spermophora*, our data strongly suggest the polyphyly of the genus and possibly five or more new genera: for four African taxa ('*S.*' *kyambura*, *tonkoui* group, *awalai* group, East African '*Spermophora*') and for East Asian '*Spermophora*'. However, several important species groups are missing in our analyses, such as South African, Madagascan, and Middle Eastern representatives. We strongly suggest including at least those groups before deciding on how to split *Spermophora*.

For *Calapnita* and *Panjange*, morphological cladistic analyses have weakly supported the monophyly of each genus, but also the existence of two distinctive subgroups in each (Huber and Nuñeza 2015, Huber 2017). The present analyses reject the monophyly of each of the two genera. Since the present analyses also strongly support the two subgroups in each genus, we feel that the pros of splitting (monophyletic genera in the most complete available analysis of Pholcidae relationships) outweighs the cons (weak morphological support of monophyly; the two subgroups of *Calapnita* are largely indistinguishable in the field).

Finally, our data strongly support the splitting of *Pholcus*, and this is largely in agreement with previous morphological cladistic analysis (Huber 2011a). The species groups that are here formally described as new genera have all been revised recently, and the diagnosis for *Pholcus* in Huber (2011a) that was explicitly valid for the 'core group' only, finally applies to the entire genus.

The present data also suggest a number of synonymies and new combinations, some of which are not formalized here.

(1) *Anopsicus* appears nested within *Modisimus*. However, neither the type species of *Anopsicus* is included in our analyses nor is a potential close relative; we conclude that the monophyly and position of *Anopsicus* both remain dubious.

(2) Our data suggest that *Coryssocnemis* and *Systenita* may both be synonyms of *Mecolaesthus*, but our taxon sampling is weak, the topology is unstable (see above), and several internal nodes in the clade have low support. The morphologically very diverse genus *Mecolaesthus* and its closest relatives clearly need more work.
(2) In most of our analyses, *Hantu* is nested within *Belisana*. For reasons detailed above we strongly doubt this result.

For other synonyms and transfers, we consider the available data strong enough to justify formal changes:

(1) The Cuban endemic genus *Platnicknia* Özdikmen & Demir, 2009 is newly synonymized with *Modisimus* Simon, 1893, syn. n. Our analyses do not include the type species *P. coxana* (Bryant, 1940) but two very similar undescribed species from near the type locality of *P. coxana* ("Cu12-99" and "Cu12-100"). Our analyses strongly support a sister group relationship of *Platnicknia* with a Hispaniolan group of leaf-dwelling *Modisimus*. Both together are deeply nested within other groups of *Modisimus* (Figure 3).
(2) The Moroccan *Pholcus agadir* is nested within *Micropholcus*. This placement receives high support in our analyses, while the previous assignment to *Pholcus* (Huber 2011a) was tentative; *Micropholcus agadir* (Huber, 2011), comb. n.
(3) The southern Indian/Sri Lankan genus *Sihala* Huber, 2011 is synonymized with *Pholcus* Walckenaer, 1805, syn. n. The position of *Pholcus ceylonicus* O. Pickard-Cambridge, 1869 (comb. re-established) in *Pholcus* had long been doubted (e.g., Brignoli 1972). The male genitalia of the two formally described species [*P. ceylonicus* and *P. alagarkoil* (Huber, 2011) comb. n.] are dramatically different from 'usual' *Pholcus* (shapes of trochanter apophysis and of femur; small and simple procursus without ventral 'knee'; bulb without uncus, with large massive appendix; Huber and Benjamin 2005, Huber 2011a). It was thus no surprise when a morphological cladistic analysis suggested a placement far away from the core group of *Pholcus* (Huber 2011a). However, our present analyses include three species of *Sihala*, two of them without missing genes, and *Sihala* was consistently placed in 'true' *Pholcus*.

Finally, the two changes at the level of subfamily suggested by all or some of our analyses are not implemented:

(1) All our analyses suggest that *Artema* is an isolated genus and single representative of Arteminae and that 'other Arteminae' should receive a new subfamily name. For reasons detailed above we consider the position of *Artema* in our analyses dubious and do not propose a new subfamily for 'other Arteminae'.
(2) Some of our analyses suggest an isolated position of the Andean genus *Priscula*: it may be either a 'basal' representative of Modisiminae or a separate subfamily. Since the relevant nodes in our analyses all receive low support values, we prefer to keep *Priscula* in Modisiminae until more convincing data become available.

Subfamily Pholcinae C.L. Koch, 1850

Nipisa Huber, gen. n.

http://zoobank.org/EB3A11CC-FE6C-4451-AA9A-8E582242C441

Calapnita phyllicola group: Deeleman-Reinhold 1986b: 212. Huber 2011a: 43. Huber 2017: 7.

Type species. *Calapnita phyllicola* Deeleman-Reinhold, 1986.

Etymology. The name is derived from the Malay word *nipis* (thin), and refers to the long and thin abdomen. Gender feminine.

Diagnosis (adapted from Huber 2017). Leaf-dwelling, pale whitish, long-legged pholcids with six eyes and long cylindrical abdomen (Huber 2017: figs 3-19). Distinguished from *Calapnita* by (1) tibia 2/ tibia 4 length >1.05 (*vs.* <0.95 in *Calapnita*); (2) ALS with eight spigots each (*vs.* two in *Calapnita*) (Huber 2017: figs 31, 41, 78); (3) proximal lateral processes on male chelicerae in 'usual' proximal position (*vs.* distal in *Calapnita*) (Huber 2017: figs 23, 35); (4) simple apophysis on male palpal trochanter (*vs.* hooked and sclerotized in *Calapnita*) (Huber 2017: figs 21, 34); (5) male palpal femur barely modified (*vs.* with series of three ventral sclerotized processes in *Calapnita*) (Huber 2017: figs 21, 34); (6) epigynum roughly rectangular or trapezoidal with folded cuticle and posterior 'knob' (*vs.* triangular with anterior 'knob' in *Calapnita*) (Huber 2017: figs 24, 32, 36, 43). For characters distinguishing *Nipisa* from similar species in other genera see Diagnosis of *Calapnita* in Huber (2017).

Distribution. Southeast Asia (Huber 2017: figs 281 and 282).

Composition. Ten species, all newly transferred from *Calapnita*: *N. anai* (Huber, 2017); *N. bankirai* (Huber, 2017); *N. bidayuh* (Huber, 2017); *N. deelemanae* (Huber, 2011); *N. kubah* (Huber, 2017); *N. lehi* (Huber, 2017); *N. phasmoides* (Deeleman-Reinhold, 1986); *N. phyllicola* (Deeleman-Reinhold, 1986); *N. semengoh* (Huber, 2017); *N. subphyllicola* (Deeleman-Reinhold, 1986).

Apokayana Huber, gen. n.

http://zoobank.org/3C3E969C-F000-4596-86B9-60F6C600C2FE

Panjange nigrifrons group: Deeleman-Reinhold and Platnick 1986: 561. Huber 2011a: 109. Huber and Leh Moi Ung 2016: 3.

Type species. *Panjange kapit* Huber, 2011.

Etymology. Named for the Apo Kayan people, one of the Dayak people groups that are spread throughout Sarawak, East Kalimantan, and North Kalimantan. Gender feminine.

Diagnosis (adapted from Huber and Leh Moi Ung 2016). Easily distinguished from *Panjange* by presence of distal male cheliceral apophyses (Huber and Leh Moi Ung 2016: fig. 18) and by ventral apophysis on male palpal femur (Huber and Leh Moi Ung 2016: fig. 30); also by absent or short epigynal scape. From representatives of *Pribumia* by ridges ventrally on procursus (Huber and Leh Moi Ung 2016: figs 17, 26, 34, 49; absent in *A. tahai*), by ventral apophysis on male palpal femur, and possibly by wide opening of palpal tarsal organ (Huber 2011a: figs 481, 686). From other similar genera on Borneo (*Calapnita*, *Leptopholcus*, *Kelabita*) by combination of: male colouration (Huber and Leh Moi Ung 2016: figs 8, 61; male ocular area and palps black; similar only in *Kelabita*), by bipartite distal apophyses on male chelicerae (Huber and Leh Moi Ung 2016: figs 35, 47; similar only in some *Calapnita*), by cylindrical rather than worm-shaped abdomen (Huber and Leh Moi Ung 2016: figs 8–15, 61–68; in contrast to *Calapnita* and *Leptopholcus*).

Distribution. Borneo (Huber and Leh Moi Ung 2016: fig. 1).

Composition. Ten species, all newly transferred from *Panjange*: *A. bako* (Huber, 2011); *A. iban* (Huber, 2011); *A. kapit* (Huber, 2016); *A. kubah* (Huber, 2016); *A. niah* (Huber, 2016); *A. nigrifrons* (Deeleman-Reinhold & Deeleman, 1983); *A. pueh* (Huber, 2016); *A. sedgwicki* (Deeleman-Reinhold & Platnick, 1986); *A. seowi* (Huber, 2016); *A. tahai* (Huber, 2011).

Pribumia **Huber, gen. n.**
http://zoobank.org/8BC96288-E983-4EAC-8015-7A6A26F5D729

Pholcus minang group: Huber 2011a: 144.

Type species. *Pholcus singalang* Huber, 2011.

Etymology. The name is derived from Pribumi, a name for native Indonesians. Gender feminine.

Diagnosis (adapted from Huber 2011a). Distinguished from other genera in Pholcinae by the combination of the following characters: elongate abdomen, six eyes, eye triads on stalks, male chelicerae with proximal and distal apophyses, distal apophyses 'divided' (consisting of two parts; Huber 2011a: figs. 640, 664), male palpal femur proximo-ventrally enlarged (Huber 2011a: figs. 628, 650), bulb with uncus, with complex sclerotized embolus, without appendix, epigynum weakly sclerotized, with small 'knob'.

Distribution. Malay Peninsula and Sumatra (Huber 2011a: fig. 626; note that *Pholcus tahai* in that figure is now in *Apokayana*).

Composition. The *Pholcus minang* group originally included seven species. Of these, *Pholcus tahai* is now in *Apokayana* (see above); the six others are newly transferred from *Pholcus*: *P. minang* (Huber, 2011); *P. singalang* (Huber, 2011); *P. hurau*

(Huber, 2011); *P. bohorok* (Huber, 2011); *P. atrigularis* (Simon, 1901); assigned tentatively: *P. diopsis* (Simon, 1901).

Tissahamia Huber, gen. n.

http://zoobank.org/14CB661D-B5F3-4DA8-B624-F02FF0AFC21E

Pholcus ethagala group: Huber 2011a: 171.

Type species. *Pholcus ethagala* Huber, 2011.

Etymology. Named for Wanniyalaeto chief Uru Warige Tissahami (1903–1996), who struggled (without success) against the government to keep the land of his ancestors. Gender feminine.

Diagnosis (adapted from Huber 2011a). Distinguished from other genera in Pholcinae by the combination of the following characters: elongate abdomen that is slightly pointed or elevated dorso-posteriorly, six eyes, eye triads on stalks, male chelicerae with proximal apophyses in frontal position, without distal apophyses (Huber 2011a: figs. 795, 811, 816), male palpal trochanter with short retrolateral and longer ventral apophyses, palpal tarsus with dorsal elongation (except *T. phui*), bulb with large and complex appendix and weakly sclerotized embolus, without uncus, procursus highly complex, epigynum weakly sclerotized, with 'knob'.

Distribution. Sri Lanka, Malay Peninsula, and Sumatra (Huber 2011a: fig. 718 – note that *Pholcus schwendingeri* in that figure is now in *Kintaqa*; Huber et al. 2016a: fig. 1).

Composition. The *Pholcus ethagala* group originally included seven species. Of these, *Pholcus schwendingeri* is now in *Kintaqa* (see below); five species have been added recently, resulting in eleven species, all newly transferred from *Pholcus*: *T. ethagala* (Huber, 2011); *T. kottawagamaensis* (Yao & Li, 2016); *T. maturata* (Huber, 2011). Assigned tentatively: *T. barisan* (Huber, 2016); *T. bukittimah* (Huber, 2016); *T. gombak* (Huber, 2011); *T. ledang* (Huber, 2011); *T. phui* (Huber, 2011); *T. tanahrata* (Huber, 2016); *T. uludong* (Huber, 2016); *T. vescula* (Simon, 1901).

Teranga Huber, gen. n.

http://zoobank.org/E67A0726-CF19-4CE3-ADFE-2D903D2778CB

Pholcus kerinci group: Huber 2011a: 166.
Pholcus domingo group: Huber et al. 2016b: 34.

Type species. *Pholcus kerinci* Huber, 2011.

Etymology. The name is derived from the Malay word *terang* (bright, light), and refers to the light colouration of the spiders. Gender feminine.

Diagnosis. Medium-sized, long-legged spiders (body length ~3.5–4.5, leg 1:~30–40) with slender elongate abdomen that is slightly elevated posteriorly (Huber 2011a: figs 606-609, Huber et al. 2016b: figs 131–139). Easily distinguished from similar relatives in other genera (*Panjange*, *Tissahamia*, *Apokayana*, *Paiwana*) by unmodified or barely modified male chelicerae Huber 2011a: fig. 722; Huber et al. 2016b: fig. 142); also by combination of: eight eyes, triads only slightly elevated; male palpal trochanter with long ventral apophysis (Huber 2011a: figs 720, 737; Huber et al. 2016b: figs 141, 158); male genital bulb without uncus but with massive appendix (Huber 2011a: figs 719, 736; Huber et al. 2016b: figs 140, 150, 157); epigynum weakly sclerotized, with numerous transversal folds, with 'knob' (Huber 2011a: figs 733, 739; Huber et al. 2016b: figs 143, 156, 159).

Distribution. Known from Indonesia (Sumatra, Java) and the Philippines (Mindanao) (Huber 2011a: fig. 718, Huber et al. 2016b: fig. 1).

Composition. The genus includes the four species originally described in the *Pholcus kerinci* and *domingo* groups. They are all newly transferred from *Pholcus*: *T. cibodas* (Huber, 2011); *T. domingo* (Huber, 2016), *T. kerinci* (Huber, 2011); *T. matutum* (Huber, 2016).

***Paiwana* Huber, gen. n.**
http://zoobank.org/BAFDACD1-7142-4909-98E0-359BDC812698

Type species. *Pholcus pingtung* Huber & Dimitrov, 2014.

Etymology. Named for the Paiwan, an indigenous people of Taiwan. Gender feminine.

Diagnosis. Large, long-legged spiders with six eyes and cylindrical abdomen (Huber and Dimitrov 2014: figs 1–4). Easily distinguished from similar species in other genera (*Teranga*, *Pholcus*, *Muruta*) by unique modifications of male chelicerae (pair of weakly sclerotized lateral apophyses and two pairs of distinctive frontal apophyses: proximal pair flat and pointed, distal pair finger-shaped, both without modified hairs; Huber and Dimitrov 2014: fig. 19); from most genera (except *Muruta*, *Calapnita*) also by shape of epigynum (roughly triangular plate, 'knob' directed towards anterior) (Huber and Dimitrov 2014: fig. 20).

Distribution. Taiwan (Huber and Dimitrov 2014: fig. 34).

Composition. Only two species newly transferred from *Pholcus*: *P. chengpoi* (Huber & Dimitrov, 2014); *P. pingtung* (Huber & Dimitrov, 2014).

***Muruta* Huber, gen. n.**
http://zoobank.org/E06DDC46-92E6-4740-BFCA-B2AD7807B9D5

Pholcus tambunan group: Huber et al. 2016b: 25.

Type species. *Pholcus tambunan* Huber, 2016.

Etymology. Named for the Murut, an indigenous ethnic group inhabiting northern inland regions of Borneo. Gender feminine.

Diagnosis (adapted from Huber et al. 2016b). The two species included in this genus are medium-sized, long-legged spiders (body length ~4, male leg 1 length: ~35–40), distinguished from other genera in Pholcinae by the combination of the following characters: elongate abdomen angular dorso-posteriorly (Huber et al. 2016b: figs 94, 98); six eyes; male chelicerae with distinctive distal apophyses (flat sclerites without modified hairs; Huber et al. 2016b: figs 103, 108, 120); most palpal structures unusually long (in particular genital bulb; Huber et al. 2016b: figs 101, 121); male bulb without uncus; epigynum weakly sclerotized, scape directed towards anterior with terminal 'knob' (Huber et al. 2016b: figs 104, 123); female internal genitalia with pair of highly distinctive three-layered telescopic tubes (Huber et al. 2016b: figs 105, 124).

Distribution. Northern Borneo (Huber et al. 2016b: fig. 1).

Composition. Only two species newly transferred from *Pholcus*: *M. tambunan* (Huber, 2016); *M. bario* (Huber, 2016).

***Meraha* Huber, gen. n.**

http://zoobank.org/14C88D64-C69D-4AB6-810B-45D93560B816

Pholcus krabi group: Huber et al. 2016a: 30.

Type species. *Pholcus krabi* Huber, 2016.

Etymology. The name is derived from the Malay word *merah* (red), and refers to the red or orange colour of the male pedipalps. Gender feminine.

Diagnosis. Medium size, light coloured pholcids with long legs and cylindrical abdomen (Huber et al. 2016a: figs 102-109); distinguished from similar species in other genera (*Kelabita*, *Apokayana*, *Teranga*, *Muruta*) by combination of: six eyes; absence of modified hairs on distal male cheliceral apophyses (Huber et al. 2016a: fig. 118); reduction of ALS spigots to two (Huber 2011a: fig. 566, Huber et al. 2016a: fig. 122); reddish to orange male palps (Huber et al. 2016a: figs 102, 106, 108). In the field they can be distinguished from most other genera (except *Kelabita*) by their domed webs relatively high among the vegetation (0.5–2 m above the ground), usually with the apex of the dome attached to the underside of a leaf.

Distribution. Mainland Southeast Asia and Borneo (Huber et al. 2016a: fig. 110).

Composition. Seven species newly transferred from *Pholcus*: *M. chiangdao* (Huber, 2011); *M. khene* (Huber, 2011); *M. kinabalu* (Huber, 2011); *M. kipungit* (Huber, 2016); *M. krabi* (Huber, 2016); *M. narathiwat* (Huber, 2016); *M. shuye* (Yao & Li, 2017).

***Kelabita* Huber, gen. n.**
http://zoobank.org/D88513D8-B25E-4CE6-94D6-B7BF215B2AA7

Pholcus andulau group: Huber et al. 2016a: 47.

Type species. *Pholcus andulau* Huber, 2011.

Etymology. Named for the Kelabit, an indigenous Dayak people of the Sarawak/North Kalimantan highlands of Borneo with a minority in the neighboring state of Brunei. Gender feminine.

Diagnosis. Medium size, light coloured pholcids with long legs, six eyes, cylindrical abdomen (Huber et al. 2016a: figs 193–196). Distinguished from similar species in other genera (*Meraha*, *Apokayana*, *Teranga*, *Muruta*) by unique, partly sclerotized embolus with strong sclerotized pointed processes (Huber 2011a: fig. 570; Huber et al. 2016a: figs 200, 210); also by combination of: male chelicerae with pair of pointed apophyses close to median line and directed toward each other (Huber 2011a: fig. 572; Huber et al. 2016a: fig. 202); ALS with eight spigots each (Huber 2016a: figs 217, 218); male palps not reddish or orange; large unsclerotized 'knob' on posterior edge of female external genitalia, directed toward anterior (Huber 2011a: fig. 573; Huber et al. 2016a: figs 203, 213). In the field they can be distinguished from most other genera (except *Meraha*) by their domed webs among the vegetation (up to 2 m above the ground), usually with the apex of the dome attached to the underside of a leaf.

Distribution. Northern Borneo (Huber et al. 2016a: fig. 153).

Composition. Only two species newly transferred from *Pholcus*: *K. andulau* (Huber, 2011); *K. lambir* (Huber, 2016).

***Kintaqa* Huber, gen. n.**
http://zoobank.org/F4C48066-1FEC-4E3B-958F-359242174F1B

Pholcus buatong group: Huber et al. 2016a: 38.

Type species. *Pholcus buatong* Huber, 2011.

Etymology. The name honours the Kintaq, a Mon-Khmer ethnic group in Thailand. Gender feminine.

Diagnosis. Medium size, light coloured pholcids with long legs, six or eight eyes, and cylindrical abdomen (Huber et al. 2016a: figs 143–152). Distinguished from similar species in other genera (*Tissahamia*, *Cantikus*, *Pribumia*) by distinctive dorsal bulging of male palpal patella (Huber 2011a: figs 581, 823; Huber et al. 2016a: fig. 155) and by epigynum with large, heavily sclerotized 'knob' (Huber et al. 2016a: figs 184, 187, 190); also by combination of: complete reduction of distal anterior apophyses on male chelicerae (Huber 2011a: figs 582, 825; Huber et al. 2016a: fig. 156); ALS with eight spigots each (Huber et al. 2016a: figs 166, 183); male palps not reddish or orange.

Distribution. Southern Thailand and northern mainland Malaysia (Huber et al. 2016a: fig. 153).

Composition. Five species, all newly transferred from *Pholcus*: *K. buatong* (Huber, 2016); *K. fuza* (Yao & Li, 2017); *K. mueangensis* (Yao & Li, 2017); *K. satun* (Huber, 2011); *K. schwendingeri* (Huber, 2011).

Cantikus Huber, gen. n.

http://zoobank.org/A71947B6-1279-4F84-8DB7-9B037D1BC70B

Pholcus halabala group: Huber 2011a: 126. Huber et al. 2016a: 3.
Pholcus quinquenotatus group: Huber 2011a: 290.

Type species. *Pholcus halabala* Huber, 2016.

Etymology. The name is derived from the Malay word *cantik* (beautiful), and refers to the colour patterns on the abdomen of several species. Gender masculine.

Diagnosis (adapted from Huber et al. 2016a): The core group of eight species (see below) includes medium-sized, long-legged spiders (body length ~3–4, male leg 1 length ~30–40); distinguished from other genera in Pholcinae by the combination of the following characters: elongate abdomen pointed dorso-posteriorly, with distinctive dorsal pattern of black and whitish or yellowish marks in life specimens (Huber et al. 2016a: figs 1–16); eight eyes; male ocular area with conspicuous modified hairs (setae), which may appear as stiff bristles or stout curved spines, or both (Huber et al. 2016a: figs 19, 23, 43); male chelicerae with proximal and distal apophyses, distal apophyses with two cone-shaped teeth (modified hairs) each (Huber et al. 2016a: fig. 28); male bulb with uncus and appendix; procursus with distinctive dorsal flap (Huber et al. 2016a: fig. 35; absent in *C. erawan*); epigynum weakly sclerotized, with 'knob'.

Distribution. Widely distributed in Southeast Asia, from Myanmar and southern China to Sumatra, Borneo, and Bali.

Composition. 27 species, all newly transferred from *Pholcus*: *C. anaiensis* (Yao & Li, 2016); *C. erawan* (Huber, 2011); *C. halabala* (Huber, 2011); *C. lintang* (Huber, 2016); *C. sabah* (Huber, 2011); *C. sepaku* (Huber, 2011); *C. ubin* (Huber, 2016); *C. zhuchuandiani* (Yao & Li, 2016).

Assigned tentatively. *C. ballarini* (Yao & Li, 2016); *C. cheni* (Yao & Li, 2017); *C. chiangmaiensis* (Yao & Li, 2016); *C. elongatus* (Yin & Wang, 1981); *C. exceptus* (Tong & Li, 2009); *C. gou* (Yao & Li, 2016); *C. khaolek* (Huber, 2016); *C. kuhapimuk* (Huber, 2016); *C. namou* (Huber, 2011); *C. pakse* (Huber, 2011); *C. phami* (Yao, Pham & Li, 2015); *C. pyu* (Huber, 2011); *C. quinquenotatus* (Thorell, 1878); *C. subwan* (Yao & Li, 2017); *C. sudhami* (Huber, 2011); *C. taptaoensis* (Yao & Li, 2016); *C. tharnlodensis* (Yao & Li, 2016); *C. wan* (Yao & Li, 2016); *C. youngae* (Huber, 2011).

Outlook

Even though the present tree of Pholcidae is a significant step forward in terms of comprehensiveness and resolution, we have identified above many weak points and aspects that need further study. Here we list a subjective 'top-ten' selection of projects that in our view might fill the most obvious gaps and provide the most valuable next steps.

1. Ninetinae external and internal relationships. The poorly known Ninetinae seem to differ from 'typical' pholcids in many respects, including body size and proportions, diversity, ecological requirements, and probably also biology. Ninetinae might be sister to all other pholcids and might have retained ancestral character states. Resolving external and internal relationships of Ninetinae is thus of particular interest but will probably require a genome-scale phylogenetic approach.
2. Position of *Artema*. Our analyses suggest an isolated position of *Artema*, not within or as sister to other Arteminae. We question this result but cannot explain it. Resolving the position of *Artema* will probably need a genome-scale phylogenetic approach.
3. Position of *Priscula*. The mysterious Andean genus *Priscula* is similar to *Artema* in including some of the largest pholcids and in defying placement in the phylogeny. As for *Artema*, a genome-scale phylogenetic approach will probably be necessary to resolve its position.
4. Andean Modisiminae. Most Pholcidae from anywhere in the world can now be quickly and reliably assigned to an existing genus. The only major exception is Modisiminae from northwestern South America, in particular Peru, Ecuador, Colombia, and Venezuela. Our analyses include a minimal sample of species from this megadiverse region that is still relatively poorly explored even at generic level.
5. Monophyly and position of *Anopsicus*. Our analyses suggest that *Anopsicus* might just be a group of dwarfed ground-dwelling *Modisimus*. However, our sample includes only three species of *Anopsicus* and none of them appears close to the type species. A much larger sample of this species-rich genus will thus be necessary to evaluate its monophyly and phylogenetic position.
6. *Holocnemus*. The type species of *Holocnemus*, *H. pluchei*, was excluded from our dataset because its position was drastically unstable in preliminary analyses. The two other species of *Holocnemus* are both included but do not group together. We suggest a genome-scale phylogenetic approach, including the three species of *Holocnemus* together with representatives of *Hoplopholcus*, *Stygopholcus*, and *Crossopriza* to solve this problem.
7. *Spermophora*. Even though many species originally described as *Spermophora* have been transferred to other or new genera, the genus continues to be polyphyletic. Our analyses suggest that five or more genera may need to be created to account for the relationships among the included species. A reanalysis of *Spermophora* should

focus on including South African and Madagascan taxa as well as Middle Eastern taxa that we predict are the closest relatives of the type species *S. senoculata*.

8. *Belisana*. *Belisana* is particularly interesting for including representatives in different microhabitats and with different types of webs. However, our sample of species is limited, web data are available for relatively few species, and several nodes in our tree have low support. Thus, a much denser sampling combined with field observations will be necessary to reconstruct microhabitat shifts and the evolution of web designs within *Belisana*.
9. *Pholcus*. Our sample includes only 18% of the described species of *Pholcus* and several species groups are entirely missing. As a result, internal relationships of this largest genus in the family remain highly uncertain and need considerably more study.
10. Missing genera. The eleven described genera that are missing from our analyses contain a total of only 24 known species, but some of them are of particular interest and should be added in future analyses. (1) *Aucana*, originally described as a Ninetinae genus, is predicted to be a member of Arteminae. (2) *Cenemus* is geographically closer to the 'southern clade' of Smeringopinae, but predicted to be a member of the 'northern clade'. (3) *Ossinissa*, possibly a close relative of cavernicole 'true' Macaronesian *Pholcus*, and thus a generic synonym. (4) *Tibetia*, probably member of Arteminae, possibly a dwarfed *Artema*. (5) *Tolteca*, predicted to be a member of the North and Central American and Caribbean clade of Ninetinae.

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Appendix 1. Summary of formal taxonomic acts, in alphabetical order.

Apokayana Huber, gen. n.; all species newly transferred from *Panjange*
Apokayana bako (Huber, 2011), comb. n.
Apokayana iban (Huber, 2011), comb. n.
Apokayana kapit (Huber, 2016), comb. n.
Apokayana kubah (Huber, 2016), comb. n.
Apokayana niah (Huber, 2016), comb. n.
Apokayana nigrifrons (Deeleman-Reinhold & Deeleman, 1983), comb. n.
Apokayana pueh (Huber, 2016), comb. n.
Apokayana sedgwicki (Deeleman-Reinhold & Platnick, 1986), comb. n.
Apokayana seowi (Huber, 2016), comb. n.
Apokayana tahai (Huber, 2011), comb. n.

Cantikus Huber, gen. n.; all species newly transferred from *Pholcus*

Cantikus anaiensis (Yao & Li, 2016), comb. n.
Cantikus ballarini (Yao & Li, 2016), comb. n.
Cantikus cheni (Yao & Li, 2017), comb. n.
Cantikus chiangmaiensis (Yao & Li, 2016), comb. n.
Cantikus elongatus (Yin & Wang, 1981), comb. n.
Cantikus erawan (Huber, 2011), comb. n.
Cantikus exceptus (Tong & Li, 2009), comb. n.
Cantikus gou (Yao & Li, 2016), comb. n.
Cantikus halabala (Huber, 2011), comb. n.
Cantikus khaolek (Huber, 2016), comb. n.
Cantikus kuhapimuk (Huber, 2016), comb. n.
Cantikus lintang (Huber, 2016), comb. n.
Cantikus namou (Huber, 2011), comb. n.
Cantikus pakse (Huber, 2011), comb. n.
Cantikus phami (Yao, Pham & Li, 2015), comb. n.
Cantikus pyu (Huber, 2011), comb. n.
Cantikus quinquenotatus (Thorell, 1878), comb. n.
Cantikus sabah (Huber, 2011), comb. n.
Cantikus sepaku (Huber, 2011), comb. n.
Cantikus subwan (Yao & Li, 2017), comb. n.
Cantikus sudhami (Huber, 2011), comb. n.
Cantikus taptaoensis (Yao & Li, 2016), comb. n.
Cantikus tharnlodensis (Yao & Li, 2016), comb. n.
Cantikus ubin (Huber, 2016), comb. n.
Cantikus wan (Yao & Li, 2016), comb. n.
Cantikus youngae (Huber, 2011), comb. n.
Cantikus zhuchuandiani (Yao & Li, 2016), comb. n.

Kelabita Huber, gen. n.; all species newly transferred from *Pholcus*
Kelabita andulau (Huber, 2011), comb. n.
Kelabita lambir (Huber, 2016), comb. n.

Kintaqa Huber, gen. n.; all species newly transferred from *Pholcus*
Kintaqa buatong (Huber, 2016), comb. n.
Kintaqa fuza (Yao & Li, 2017), comb. n.
Kintaqa mueangensis (Yao & Li, 2017), comb. n.
Kintaqa satun (Huber, 2011), comb. n.
Kintaqa schwendingeri (Huber, 2011), comb. n.

Meraha Huber, gen. n.; all species newly transferred from *Pholcus*
Meraha chiangdao (Huber, 2011), comb. n.
Meraha khene (Huber, 2011), comb. n.
Meraha kinabalu (Huber, 2011), comb. n.

Meraha kipungit (Huber, 2016), comb. n.
Meraha krabi (Huber, 2016), comb. n.
Meraha narathiwat (Huber, 2016), comb. n.
Meraha shuye (Yao & Li, 2017), comb. n.

Micropholcus agadir (Huber, 2011), comb. n., transferred from *Pholcus*

Modisimus coxanus (Bryant, 1940), comb. n., newly transferred from *Platnicknia*
Modisimus incertus (Bryant, 1940), comb. n., newly transferred from *Platnicknia*

Muruta Huber, gen. n.; all species newly transferred from *Pholcus*
Muruta bario (Huber, 2016), comb. n.
Muruta tambunan (Huber, 2016), comb. n.

Nipisa Huber, gen. n.; all species newly transferred from *Calapnita*
Nipisa anai (Huber, 2017), comb. n.
Nipisa bankirai (Huber, 2017), comb. n.
Nipisa bidayuh (Huber, 2017), comb. n.
Nipisa deelemanae (Huber, 2011), comb. n.
Nipisa kubah (Huber, 2017), comb. n.
Nipisa lehi (Huber, 2017), comb. n.
Nipisa phasmoides (Deeleman-Reinhold, 1986), comb. n.
Nipisa phyllicola (Deeleman-Reinhold, 1986), comb. n.
Nipisa semengoh (Huber, 2017), comb. n.
Nipisa subphyllicola (Deeleman-Reinhold, 1986), comb. n.

Paiwana Huber gen. n.; all species newly transferred from *Pholcus*
Paiwana chengpoi (Huber & Dimitrov, 2014), comb. n.
Paiwana pingtung (Huber & Dimitrov, 2014), comb. n.

Pholcus alagarkoil (Huber, 2011), comb. n., newly transferred from *Sihala*
Pholcus ceylonicus O. Pickard-Cambridge, 1869, comb. re-established, transferred from *Sihala*

Platnicknia Özdikmen & Demir, 2009 = *Modisimus* Simon, 1893, syn. n.

Pribumia Huber, gen. n.; all species newly transferred from *Pholcus*
Pribumia atrigularis (Simon, 1901), comb. n.
Pribumia bohorok (Huber, 2011), comb. n.
Pribumia diopsis (Simon, 1901), comb. n.
Pribumia hurau (Huber, 2011), comb. n.
Pribumia minang (Huber, 2011), comb. n.
Pribumia singalang (Huber, 2011), comb. n.

Sihala Huber, 2011 = *Pholcus* Walckenaer, 1805, syn. n.

Teranga Huber gen. n.; all species newly transferred from *Pholcus*
Teranga cibodas (Huber, 2011), comb. n.
Teranga domingo (Huber, 2016), comb. n.
Teranga kerinci (Huber, 2011), comb. n.
Teranga matutum (Huber, 2016), comb. n.

Tissahamia Huber gen. n.; all species newly transferred from *Pholcus*
Tissahamia barisan (Huber, 2016), comb. n.
Tissahamia bukittimah (Huber, 2016), comb. n.
Tissahamia ethagala (Huber, 2011), comb. n.
Tissahamia gombak (Huber, 2011), comb. n.
Tissahamia kottawagamaensis (Yao & Li, 2016), comb. n.
Tissahamia ledang (Huber, 2011), comb. n.
Tissahamia maturata (Huber, 2011), comb. n.
Tissahamia phui (Huber, 2011), comb. n.
Tissahamia tanahrata (Huber, 2016), comb. n.
Tissahamia uludong (Huber, 2016), comb. n.
Tissahamia vescula (Simon, 1901), comb. n.

Supplementary material 1

Figure S1. Maximum-likelihood tree of the complete set of taxa inferred with IQ-TREE

Authors: Bernhard A. Huber, Jonas Eberle, Dimitar Dimitrov

Data type: molecular data

Explanation note: This tree is identical to the one shown in Figs 2–12 except that it includes all outgroups and all support values are shown (in the sequence SBS / RBS / SH-like aLRT).

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Link: https://doi.org/10.3897/zookeys.788.22781.suppl1

Supplementary material 2

Figure S2. Maximum-likelihood tree of the complete set of taxa inferred with RAxML

Authors: Bernhard A. Huber, Jonas Eberle, Dimitar Dimitrov

Data type: molecular data

Explanation note: Support values as in Figure S1.

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Supplementary material 3

Figure S3. Maximum-likelihood tree (RAxML) of a reduced set of taxa (excluding rogue taxa with RogueNaRok)

Authors: Bernhard A. Huber, Jonas Eberle, Dimitar Dimitrov

Data type: molecular data

Explanation note: In the text we refer to this tree as 'RogueNaRok tree'. Support values: RBS.

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Link: https://doi.org/10.3897/zookeys.788.22781.suppl3

Supplementary material 4

Figure S4. Maximum-likelihood tree (RAxML) of a reduced set of taxa (excluding taxa for which less than four genes were available)

Authors: Bernhard A. Huber, Jonas Eberle, Dimitar Dimitrov

Data type: molecular data

Explanation note: In the text we refer to this tree as '4+ genes tree'. Support values as in Figure S1.

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